MULTITUBERCULATE MAMMALS FROM THE UPPER JURASSIC PURBECK LIMESTONE FORMATION OF SOUTHERN ENGLAND

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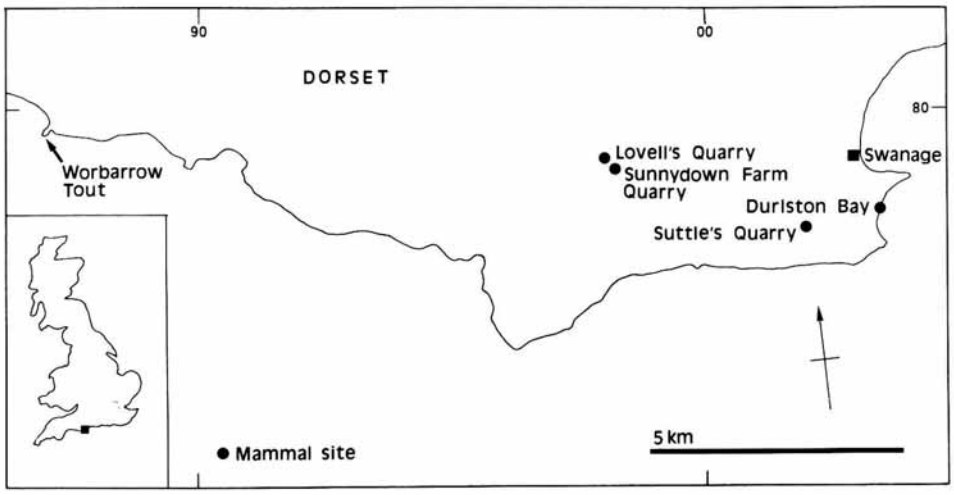
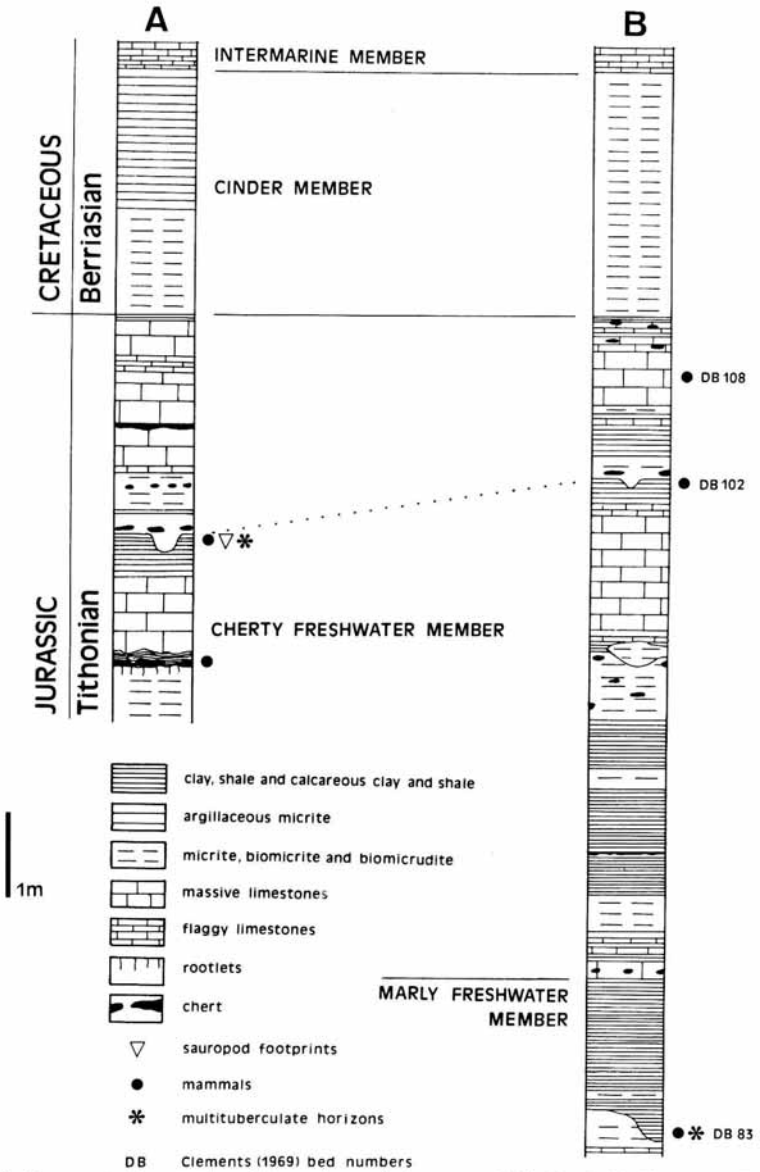
ABSTRACT. The multituberculate suborders: Paulchoffatoidea (Hahn, 1969, new rank) and Plagiaulacoidea (Simpson, 1925), plagiaulacoid families Plagiaulacidae (with two subfamilies Plagiaulacinae and Eobaatarinae) and Allodontidae are re-diagnosed. The Arginbaataridae is assigned to a suborder *incertae sedis*. It is demonstrated that *Plioprion* Cope, 1884, based on lower jaws, is a junior synonym of *Bolodon* Owen, 1871, based on upper jaws. A dentary fragment and twenty-five isolated multituberculate teeth from the Upper Jurassic Purbeck Limestone Formation are described. In one case seven teeth found in one sample are regarded as belonging to the same individual. *Bolodon* and *Plagiaulax* Falconer, 1857 are assigned to the Plagiaulacinae; the systematic position of *Zofiabaatar* Bakker and Carpenter, 1990 is uncertain; *Ctenacodon* Marsh, 1879 and *Psalodon* Simpson, 1926 are assigned to the Allodontidae. Two taxa are erected: *Gerhardodon purbeckensis* gen. et sp. nov. and *Sunnyodon notleyi* gen. et sp. nov., assigned to the Paulchoffatiidae. An upper premolar with three main cusps, additional cusps, cuspules and pits, is different from any hitherto known and is identified as ?Plagiaulacinae gen. et sp. indet. The new taxa are notably smaller than those previously known from the Purbeck Limestone Formation of England, probably the result of the screen-washing method employed in their collection.

THE first significant collection of mammals from the Purbeck Limestone Formation was made by S. H. Beckles from his legendary excavation in 1857 on the cliffs of Durlston Bay, Swanage, Dorset (Text-fig. 1). The excavation was in part due to the encouragement of Richard Owen and was



TEXT-FIG. 1. Map showing the location of the Purbeck Limestone Formation localities mentioned in the text.

[Palaeontology, Vol. 35, Part 1, 1992, pp. 95–126. 5 pls.]



TEXT-FIG. 2. Representative stratigraphic sections of the part of the Purbeck Limestone Formation at Sunnydown Farm Quarry (A) redrawn from Ensom (1988), and Durlston Bay (B) based on Clements (1969).

graphically described by Charles Kingsley (1857). Owen had studied the earlier discoveries, which included mammals, made in Durlston Bay by P. B. Brodie and C. Wilcox (Owen 1854). The collection made by Beckles formed the basis of Owen's (1871) account of the Purbeck mammals in the monograph 'Fossil Mammalia of the Mesozoic Formations'.

Since Beckles's pioneering work a number of attempts have been made to relocate his 'Mammal Bed'. Two of these, by H. Willett in 1880 and W. Heap between 1946 and 1949, were recorded by E. W. Willett and H. Willett (1881), and Heap (1958), respectively, who, despite considerable expenditure of time and money, found only five further jaws. From the time of the first discoveries the coastal section has remained the focus of endeavour and further specimens have been recovered by individual collectors and university-based researchers.

The mammalian fauna recovered includes multituberculates (see Hahn 1978*a*, and Clemens and Kielan-Jaworowska 1979 for reviews), which have been described by Falconer (1857, 1862), Owen (1871), and Simpson (1928).

Until now, the principal source of Purbeck mammals is believed to have been the so-called 'Mammal Bed', Bed 83 of Clements (1969), which lies within the Marly Freshwater Member of the Purbeck Limestone Formation (Text-fig. 2). Owen (1871, fig. 4) also records a mammal as coming from the 'Feather Bed', Bed 108 of Clements (1969) which lies in the overlying Cherty Freshwater Member, also of the Purbeck Limestone Formation. Exposures of these strata rarely occur in quarries inland from Durlston Bay. Routine fieldwork in Sunnydown Farm Quarry, Sunnydown Farm, near Langton Matravers, Swanage, Dorset (NGR SY 9822 7880), by one of us (P.C.E., then at the Dorset County Museum) and Dr W. A. Wimbledon (Nature Conservancy Council) during the summer of 1986 led to the discovery of a diverse dinosaur footprint fauna, including the first sauropod tracks to be recorded in the Purbeck Limestone Formation. Subsequent work on the site produced a rich vertebrate fauna of fish, amphibians, reptiles and mammals. Brief accounts of these discoveries were given by Ensom (1987, 1988, 1989).

The collection of Purbeck mammalian teeth so far recovered from the Sunnydown Farm contains members of the Triconodonta, Docodonta, Symmetrodonta, Peramura and Multituberculata. This paper is a description of the multituberculate material so far recovered.

The terminology employed in the present paper is that of Kielan-Jaworowska *et al.* (1987). Abbreviations include: BMNH, Natural History Museum, London (previously British Museum (Natural History)); DORCM, Dorset County Museum, Dorchester, Dorset; PIN, Palaeontological Institute, USSR Academy of Sciences, Moscow; YPM, Yale Peabody Museum, New Haven; I, i, P, p, M, m, upper and lower incisor, premolar and molar, respectively; d, deciduous.

STRATIGRAPHY AND LOCALITIES

Sunnydown Farm Quarry provides an exposure in the upper part of the Cherty Freshwater Member (uppermost Lulworth Beds of Casey 1963) lying below the Cinder Member (Text-fig. 2), the base of which currently marks the boundary of the Jurassic and Cretaceous periods in Southern England (Rawson *et al.* 1978, following Casey 1963).

The Cherty Freshwater Member is represented by a sequence of clays, calcareous clays, biomicrites and biosparrudites. The limestones often contain nodules of chert. The footprints were made in a fine-grained mixture of smectite and illite (West 1988) and are preserved as casts on the base of the overlying cherty biomicrite. This limestone is referred to as the 'Cap' by quarrymen and can be correlated with bed 103 (Clements 1969) in Durlston Bay (NGR SZ 035780) and bed 117 (Ensom 1985) at Worbarrow Tout (NGR SY 869 796). The underlying vertebrate-rich clay can accordingly be correlated with bed 102 in Durlston Bay and 116 at Worbarrow Tout. At the former locality this is *c.* 7·5 m above the 'Mammal Bed' (Clements 1969). Below the underlying 'New Vein' (= bed 101 in Durlston Bay) is a very carbonaceous clay, rich in coprolites and containing a vertebrate fauna which includes mammals, though no multituberculates have so far been recorded.

Following the recovery of mammals from the clay below the 'Cap', samples were taken from the same horizon in Durlston Bay, Suttle's Quarry (NGR SZ 020777) and Lovell's Quarry (NGR SY

980790), 5·25 km and 4 km ESE and 300 m NW of Sunnydown Farm Quarry respectively (Text-fig. 1). All samples collected yielded a similar fauna. The teeth of multituberculates were present in samples from all three quarry sites. Tridactyl dinosaur footprints were present at Durlston Bay, Lovell's and Sunnydown Farm Quarries but not observed at Suttle's Quarry. Sauropod tracks have only been recorded at Lovell's and Sunnydown Farm Quarries. A 1·4 kg sample of clay taken at the equivalent horizon with tridactyl footprints at Worbarrow Tout (11 km WNW) yielded some vertebrate remains though no mammalian remains were observed.

PALAEOENVIRONMENT

The conditions that existed during the deposition of the Purbeck Limestone Formation were generally brackish or freshwater, though there are occasional appearances of an almost normal marine fauna, e.g. in the Cinder and Scallop Members. With a view to establishing the nature of the environments the abundant invertebrate faunas have been the subject of a number of studies.

Examples are the papers on ostracods and faunicycles by Anderson (1985) and the palaeoecology of the molluscs and their relationship to ostracod biostratigraphy by Morter (1984). Carbon isotope ratios were used by Allen and Keith (1965) to study palaeosalinity in these strata.

West (1988) gives a detailed description of both the clay and the overlying limestone at Sunnydown Farm Quarry drawing the conclusion that they were deposited in environments with 'very low' and 'low' salinities respectively. West suggests that the clays represent extensive mud flats bordering a freshwater lake. The presence of dinosaurs is evident from the considerable number of footprints recorded at all sites but one. This would suggest emergent or at least shallow water deposition for the clays. No evidence of mudcracking has been noted in the clays or on the base of the overlying 'Cap'. The remarkable similarities between sediment type and palaeontology observed at the sites on this strike exposure of 16 km give some idea of how extensive this freshwater lake may have been.

The presence of reworked vertebrate material from earlier sediments cannot be ruled out; significant quantities of silicified wood are present in the samples and this is considered to have been derived. The presence within individual samples of teeth, which have come from the same dentition, points to at least some of the material suffering minimal transport within the environment of deposition.

MATERIALS AND METHODS

The samples collected at Sunnydown Farm Quarry consisted of approximately 3 tonnes of clay dug from the floor of the quarry after the 'Cap' bed had been removed. Normally the top 2–4 cm were collected in samples up to *c.* 35 kg. Each sample was from beneath one or more slabs of the 'Cap'. The slabs were mapped and numbered and the sample sacks carried the same numbers. Single sample numbers were allocated to each sack. Samples were kept separate so that any associations of bones and teeth would be preserved.

The fissured limestone overlying the clay and steep quarry faces on three sides resulted in inevitable contamination of samples though every care was taken to keep this to a minimum. In addition the fractured 'Cap' often spalled lower surfaces which were removed with the clay samples and only recovered later as the coarse fraction during sieving.

The samples were removed from the site and dried before sieving. The first samples were processed through 20 cm brass test sieves down to aperture size of 0·3 mm. A bulk processing machine constructed to the design of Ward (1981) permitted the remaining samples to be sieved with great efficiency through a stainless steel mesh with an aperture size of 0·33 mm. Approximately 5% of the original sample remained after sieving. The residues were graded and then picked under a binocular microscope using a gridded sorting tray. Only a small proportion of the total sample has so far been picked.

The descriptions that follow are based mostly on the new collection housed in the Dorset County Museum, and the specimens described are from the Cherty Freshwater Member of the Purbeck Limestone Formation from three localities: Sunnydown Farm and Lovell's Quarries, both near Langton Matravers, and Suttle's Quarry near Swanage. The specimens from the old collection from the 'Mammal Bed', Marly Freshwater Member, Durlston Bay near Swanage (deposited in the BMNH) are discussed mostly under Comparisons, but scanning electron micrographs of the epoxy resin casts of some of them, and drawings, are published for comparative purposes.

We restrict the synonymies to publications in which the specimens are illustrated.

DIAGNOSES OF SUPRAGENERIC TAXA

The high-level taxonomy of the Late Jurassic and Early Cretaceous multituberculates are misleading. We are aware that the suborders Paulchoffatoidea and Plagiaulacoidea and some of the families assigned to them are possibly paraphyletic groups; however, because of the fragmentary nature of the material we have found it impossible to treat them cladistically. We redefine the suborders Paulchoffatoidea (new rank) and Plagiaulacoidea and the families and subfamilies of the latter, as far as the new material described in this paper allows us to do so. We hope that this material will help in future to recognize the true relationships between these suborders and families.

In the diagnoses given below we use the following abbreviations: All., Allodontidae; Arg., Arginbaataridae; Eobn., Eobaatarinae; multis, multituberculates; Paul., Paulchoffatoidea; Plag., Plagiaulacoidea; Plagn., Plagiaulacinae; Plagd., Plagiaulacidea; Ptil., Ptilodontoidea; Taen., Taeniolabidoidea.

Suborder PAULCHOFFATOIDEA (Hahn, 1969), new rank

Revised diagnosis. Dental formula: 3,1–0,5–4,2/1,0,4–3,2. Differs from Plag. (except Plagn.), Ptil. and Taen. in having I3 3- to 4-cusped. Differs from Plag., Ptil. and Taen. in having M1 without posterolingual ridge or third row of cusps. Differs from Plag. in having M2 with 2–3:3–6 cusps and no anterobuccal wing. Differs from all other multis in having p1–p3 in buccal view oval or quadrangular rather than triangular; p3 almost as long as p4, p3 with a row of buccal cusps. Shares with Plag. parallel-sided p4 (plesiomorphy), but differs in having only 4 serrations in p4. Differs from Plagd., Ptil. and Taen. in having m1 with anterior cingulum with cuspules and enlarged buccal cusp. Differs from all multis in having m2 basin-like, with only one anterolingual cusp and in having a rudimentary coronoid. Differs from Ptil. and Taen. (whether from Plag. unknown) in having enamel tentatively referred to as ?aprismatic.

Stratigraphic and geographical range. Middle Jurassic–Early Cretaceous of Europe, Early Cretaceous of North Africa.

Remarks. We assign to this suborder all the taxa from the Late Jurassic of Portugal assigned by Hahn and Hahn (1983) and Hahn (1987, 1988) to the Paulchoffatiidae: isolated teeth identified by Hahn and Hahn (1983) as Paulchoffatiidae, gen. et sp. indet. 3, and tentatively Paulchoffatiidae?, gen. et sp. indet. 4, from the Middle Jurassic of England; *Gerhardodon* gen. nov. and *Sunnyodon* gen. nov. from the Purbeck Limestone Formation of England; *Parendotherium* Crusafont-Pairo and Adrover from the Early Cretaceous of Spain and Hahnodontidae Sigogneau-Russell from the Early Cretaceous of Morocco (Sigogneau-Russell 1991). *Mojo* Hahn, Lepage and Wouters, 1987 from the Upper Triassic of Belgium is poorly known and is not included here. A discussion on the taxonomy of the paulchoffatoid taxa is beyond the scope of the present paper.

Suborder PLAGIAULACOIDEA (Simpson, 1925), Hahn, 1969

Revised diagnosis. Dental formula: 3,0,5–4,2/1,0,4–3,2. Differs from some Paul., Ptil. and Taen. in having I3 2- or 3-cusped. Differs from Paul. in having M1 with an incipient wing-like posterolingual

ridge and smaller number of cusps in M2 (2–3:3). Differs from Paul. but shares with other multis p1–p3 triangular in buccal aspect and p3 without buccal cusps. Shares with Paul. parallel-sided p4 (plesiomorphy), but differs in having p4 1·5–2 times longer than p3 rather than subequal in length and greater number (5–8) serrations on p4. Differs from Paul. but shares with other multis m2 with a middle groove. Differs from Ptil., Taen. and Arg. in having discrete cusps (2–3) in m2 only in a lingual row and incipient cusps in buccal row in Plagd. (more discrete buccal cusps in All.). Differs from Paul. but shares with other multis lack of coronoid bone in known taxa.

Families. Plagiaulacidae Gill, 1872; Allodontidae Marsh, 1889.

Stratigraphic and geographical range. Late Jurassic to Early Cretaceous of Europe, Late Jurassic of North America, Early Cretaceous of Asia.

Family PLAGIAULACIDAE Gill, 1872

Revised diagnosis. Differs from All. in having I3 3-cusped (plesiomorphy); P4 and P5 relatively longer in relation to M1, P4 with a row of buccal cuspules; posterolingual wing in M1 relatively larger; anterobuccal incipient cingulum on M2; p4 about twice as long as p3, with 6–8 serrations; m1 without an enlarged buccal cusp; m2 without obvious buccal cusps, separated only lingually by irregular grooves. Differs from all other multis in having a characteristic 'ornamentation' of comma-shaped pits and grooves. Differs from All. and most other multis in a tendency of basal parts of molar cusps to coalesce in peripheral aspect.

Subfamilies. Plagiaulacinae Gill, 1872; Eobaatarinae Kielan-Jaworowska, Dashzeveg and Trofimov, 1987.

Geographical and stratigraphic range. Late Jurassic to Early Cretaceous of Europe; ?Late Jurassic of North America; Early Cretaceous of Asia.

Subfamily PLAGIAULACINAE Gill, 1872

Revised diagnosis. More plesiomorphic subfamily than Eobn., from which it differs in having P5 with buccal cuspules; M1 with smaller posterolingual ridge; lower incisor (in most taxa) with complete enamel, but limited enamel in North American 'plagiaulacoid'; p4 as a rule with a row of buccal cusps (but single cusp in *Bolodon osborni*); m1 and m2 symmetrical; enamel referred to as ?preprismatic (not gigantoprismatic).

Genera. *Plagiaulax* Falconer, 1857; *Bolodon* Owen, 1871; ?new genera to be erected for '*Bolodon*' *falconeri*, '*Bolodon*' *elongatus* and ?*Zofiabaatar* Bakker and Carpenter, 1990.

Geographical and stratigraphic range. Late Jurassic Europe, ?Late Jurassic of North America.

Remarks. *Plioprion* Cope, 1884 was erected as a monotypic genus to include *Plagiaulax minor* (Falconer, 1857), a species classified by us as *Bolodon minor* (Falconer). We demonstrate that *Ctenacodon ?minor* (Falconer) (Simpson 1928, p. 40, *recte*: *Plioprion ?minor*) is a junior synonym of *Bolodon osborni*. *Plioprin* Cope, 1884 is therefore a junior synonym of *Bolodon* Owen, 1871. Two more species were assigned to *Plioprion* by Hahn and Hahn (1983): *Plioprion? dawsoni* known from single m2 that according to Clemens (1963) may not be a mammal tooth, and *Plioprion? falconeri* (Owen, 1871) which is a lower jaw taxon. As the upper teeth of this species are not known, it cannot be demonstrated whether it belongs to *Bolodon* or to a new genus, and we refer to it as '*Bolodon*' *falconeri*. *Zofiabaatar* (Bakker and Carpenter, 1990) from the Morrison Formation of North America, assigned to an uncertain family, is related to the Plagiaulacidae in having p3 reduced in length, as long as a half of p4 (plagiaulacid apomorphy), but shares with Allodontidae a paulchoffatiid-like structure of m1 (plesiomorphy); it is not known whether it shares other features

characteristic of European plagiaulacines. A new subfamily or family should be erected for it. Another North American Morrison Formation 'plagiaulacoid' with limited enamel on lower incisor, recently reported by Engelmann *et al.* (1990), may also be a member of the Plagiaulacidae.

Subfamily EOBAATARINAE Kielan-Jaworowska, Dashzeveg and Trofimov, 1987

Revised diagnosis. Differs from most Plagn. (except North American 'plagiaulacoid') in having limited enamel on the lower incisor, m1 and m2 asymmetrical, shorter lingually than buccally, P5 without buccal cuspules and M1 with more prominent posterolingual ridge. Differs from Paul., Plagn., and Ptil., but shares with Arg. and Taen. gigantoprismatic enamel.

Genera. *Loxaulax* Simpson, 1928; *Eobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987; ?*Monobaatar* Kielan-Jaworowska, Dashzeveg and Trofimov, 1987.

Geographical and stratigraphic range. Early Cretaceous of Europe and Asia.

Remarks. Kielan-Jaworowska *et al.* (1987) assigned the Eobaataridae to the Taeniolabidoidea because of the limited enamel on the lower incisor and gigantoprismatic enamel regarded as taeniolabidoid apomorphies. They made it clear, however, that the Eobaataridae is very close to the Plagiaulacidae. Limited enamel on the lower incisor has been found recently in a 'plagiaulacoid' from North America (Engelmann *et al.* 1990) and cannot be regarded as a taeniolabidoid apomorphy. Enamel structure in multituberculate taxa is so far poorly understood, and one cannot be sure whether one can make systematic assignments on its basis. Our present comparisons show that the Eobaataridae (*sensu* Kielan-Jaworowska *et al.* 1987) and the Plagiaulacinae (as defined herein) are closer to each other than any of them is to the Allodontidae. Therefore we assign the Eobaatarinae (new rank) to the Plagiaulacidae.

Family ALLODONTIDAE Marsh, 1889

Revised diagnosis. Differs from Plagd. in having 2-cusped I3; P4 and P5 relatively shorter in relation to the length of M1 (plesiomorphy), with one or no buccal cuspules; posterolingual ridge in M1 very small; anterobuccal cingulum in M2 uncertain, possibly lacking; p4 about 1·5 times (instead of twice) as long as p3, with 5–6 serrations and a row of buccal cusps; m1 somewhat Paul.-like in having an enlarged middle cusp in buccal row; m2 with 3: 3 cusps, cusps more discrete than in Plagd., in buccal row clearly separated on lingual aspect, possibly coalesced buccally. No grooves and pits on molars characteristic of Plagd.

Genera. *Ctenacodon* Marsh, 1879; *Psalodon* Simpson, 1926.

Stratigraphic and geographical range. Late Jurassic of North America.

Remarks. The type genus of the Allodontidae is *Allodon* Marsh, 1881, a junior subjective synonym of *Ctenacodon* Marsh, 1879.

Suborder *incertae sedis*

Family ARGINBAATARIDAE Hahn and Hahn, 1983

Revised diagnosis. Differs from all multis in having very large p4 with limited enamel, rotating anteroventrally during the ontogeny over the worn p3 and p2, which disappear. Shares with Paul., some Plagn. and Ptil. lower incisor completely covered with enamel (plesiomorphy). Shares with some Paul. presence of canine (plesiomorphy). Differs from Plgd. and shares with All. P4 and P5 without buccal cuspules. Differs from Plagd. in having distinct conical cusps on lower and upper molars. Shares with Plag. incipient posterolingual ridge in M1. Differs from Plgac. in having molar cusps smooth or weakly striated. Shares with Eobn. and Taen. gigantoprismatic enamel.

Genus. Arginbaatar Trofimov, 1980.

Stratigraphic and geographical range. Early Cretaceous of Asia.

Remarks. Kielan-Jaworowska *et al.* (1978) assigned the Arginbaataridae to the ?Plagiaulacoidea, but stated that it differs in the structure of p4 from the plagiaulacoids and from all other multituberculates, warranting inclusion in a suborder of its own. As the upper and lower jaws of Arginbaataridae have not been found together and were only tentatively matched by Kielan-Jaworowska *et al.* (1987), we think that the erection of a new suborder for the Arginbaataridae would be premature.

Discussion

The apomorphies of the Paulchoffatoidea are: ?the structure of I3 with 3–4 cusps; the structure of m1 with anterior cingulum with cuspules and two rows of cusps in which one buccal cusp is clearly enlarged, and the structure of m2 which is basin-like with only one antero-lingual cusp. These types of teeth have not been so far found in the Haramiyiidae, although *Haramiya*, group I bis (Sigogneau-Russell 1989 and references therein), resembles m1 of Paulchoffatoidea. As demonstrated by Krause and Hahn (1990), all paulchoffatiids (including Paulchoffatiinae) have the crown of M2 offset lingually relative to that in M1, as is characteristic of plagiaulacids and all other multituberculates.

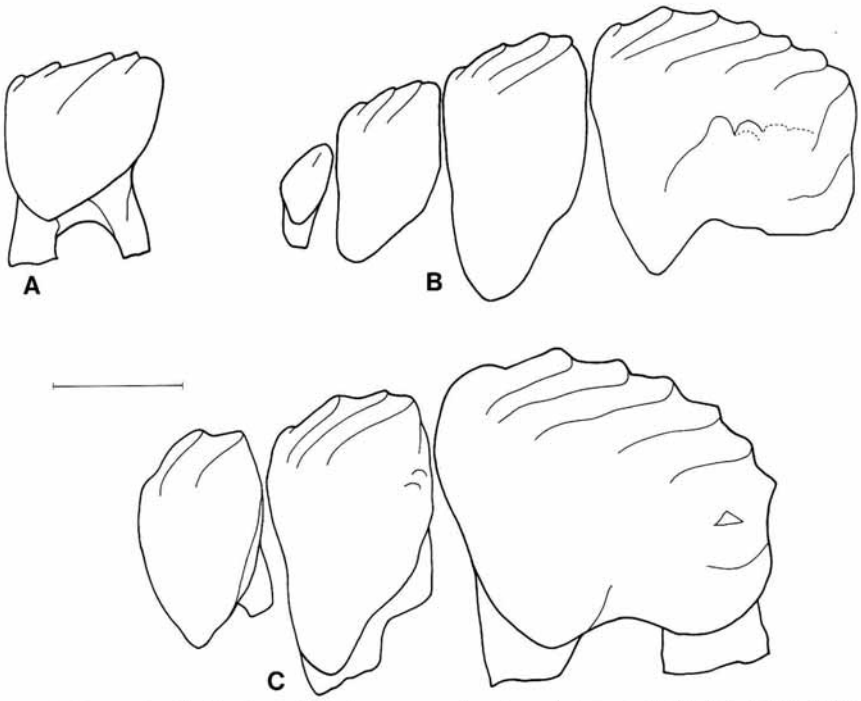
Some of the paulchoffatoid apomorphies are retained in plagiaulacoid taxa, e.g. three-cusped I3 in Plagiaulacidae and somewhat paulchoffatoid-like m1 in Allodontidae, and are primitive characters in these groups.

The apomorphies of the Plagiaulacoidea are: the triangular shape of p1–p3, disappearance of buccal cusps in p3, increase in the number of serrations in P4, increase of the length of p4 in relation to p3, appearance of the middle groove in m2, appearance of the postero-lingual ridge in M1 and reduction of the number of cusps in M2. M1 in Paulchoffatoidea has only two rows of cusps, although in *Henkelodon* (see Hahn 1977, fig. 10) there appears to be a tiny, although uncertain posterolingual ridge, not so obvious as in Plagiaulacoidea (this tooth was referred to by Hahn 1977 as M2, which is M1 – an opinion with which Professor Gerhard Hahn now agrees, personal communication).

The apomorphies of the Plagiaulacidae are: an increase of the length of P4 and P5 in relation to the length of M1, an appearance of an incipient anterobuccal wing in M2, appearance of irregular grooves that divide the buccal rounded ridge in m2 (Text-fig. 4), the 'ornamentation' of comma-shaped pits and grooves on the molars. In the structure of the upper premolars and molars the Plagiaulacidae are perhaps most reminiscent of the paulchoffatiid *Henkelodon* (assigned to the Kuehneodontinae, see Hahn 1977), which has a row of buccal cuspules on P4 and P5 in addition to the two rows of cusps. The M2 of *Henkelodon* is not known. Another paulchoffatoid genus that has P4 and P5 similar to those in the Plagiaulacidae is *Kielanodon*, assigned by Hahn (1987) to an uncertain subfamily in the Paulchoffatiidae. The upper molars and lower jaw of *Kielanodon* are not known.

The apomorphies of the Allodontidae are: two-cusped I3 and the presence of two rows of distinct cusps in m2. There are three buccal cusps in m2 in the Allodontidae, separated medially, but it is not certain whether they coalesce buccally. As far as the structure of the lower premolars is concerned the Allodontidae is more plesiomorphic than the Plagiaulacidae, as the shortening of the length of p3 in relation to the length of p4 is smaller than in the Plagiaulacidae. In Allodontidae P4 and P5 are relatively shorter in relation to the length of M1 than in the Plagiaulacidae, which is also a plesiomorphic feature, characteristic of most paulchoffatoid taxa. m1 in Allodontidae is also more plesiomorphic than in the Plagiaulacidae in having an enlarged second cusp of the buccal row (similar to that in Paulchoffatoidea), while in the Plagiaulacidae the two buccal cusps in m1 are of subequal size.

The grooves on molars characteristic of the Plagiaulacidae are also characteristic of (but less



TEXT-FIG. 3. Camera lucida drawings of the lower premolars, buccal view. A, *Gerhardodon purbeckensis* gen. nov., sp. nov.; left ?p3; DORCM GS 19; holotype. B, *Bolodon minor* (Falconer); right p1–p4; reversed, based on epoxy resin cast of BMNH 47729. C, *Bolodon osborni* Simpson; left p2–p4; p4 based on epoxy resin cast of left tooth BMNH 48399, p3 on DORCM GS 202, p2 on DORCM GS 204. Scale = 1 mm.

obvious in) the Argentinean Late Cretaceous *Ferugliotherium* (Bonaparte 1986). The peripheral (buccal, posterior, lingual and possibly anterior) cusps on M1 of *Ferugliotherium* tend to coalesce basally as characteristic of the Plagiaulacidae. The transverse grooves also occur in the molars of ptilodontoids; these are more regularly distributed than in the plagiaulacines and eobaatarines and there is little or no coalescence. In Taeniolabidoidea such grooves are generally absent; even when present they are not as well developed as in ptilodontoids, except perhaps in *Microcosmodon*.

SYSTEMATIC PALAEONTOLOGY

Suborder PAULCHOFFATOIDEA Hahn, 1969, new rank
Family ?PAULCHOFFATIIDAE Hahn, 1969
Subfamily *incertae sedis*
Genus GERHARDODON gen. nov.

Etymology. In honour of Professor Gerhard Hahn (Marburg) in recognition of his work on multituberculates and Greek *odous*, meaning tooth.

Diagnosis. As for the only species *Gerhardodon purbeckensis* sp. nov.

Gerhardodon purbeckensis sp. nov.

Plate 1, figs 1–5; Text-fig. 3A.

Etymology. Occurring in the Purbeck Limestone Formation.
Holotype. DORCM GS 19 (sample 95), left ?p3 (Pl. 1, figs 3–5; Text-fig. 3A).

Type horizon and locality. Purbeck Limestone Formation, Cherty Freshwater Member, Sunnydown Farm Quarry near Langton Matravers.

Additional material. There are two more specimens in the same sample (no. 95) that may belong to the same individual: DORCM GS 20, a right ?p3 is almost identical to DORCM GS 19 and conspecific with it; DORCM GS 21, the anterior part of a ?right P4 or P5 is described under cf. *Gerhardodon purbeckensis*.

Diagnosis. ?p3 differs from p3 of *Kuehneodon* and *Guimarotodon* (and possibly from other paulchoffatiid taxa in which this tooth is abraded) in having almost transversal (rather than vaulted) upper margin, in being roughly trapezoidal and slightly longer than high, rather than taller and roughly oval or quadrangular. Differs from p3 in other paulchoffatiid genera in having the distance between the second and third serrations greater than between the others and the third ridge the longest. Buccal cusps which occur in p3 of Portuguese paulchoffatiids are absent.

Description. Left ?p3 DORCM GS 19, in buccal aspect is irregular, roughly trapezoidal, taller anteriorly than posteriorly, 1·0 mm long and 0·9 mm high. The upper margin is nearly straight, the exodaenodont lobe weakly pronounced. There are four serrations and four weak ridges, the first in both buccal and lingual aspects being hardly discernible. The distance between the second and the third serration is one and a half times longer than between the first and the second and twice as long as between the third and fourth. The ridge of the third serration in both aspects is notably longer and more prominent than the others. The lingual side is less tall than the buccal, roughly oval, and elongated longitudinally. Right ?p3 DORCM GS 20, is almost identical with DORCM GS 19, differing only in having a slightly more elongated exodaenodont lobe; the tooth is 0·9 mm long and 1·0 mm high in buccal aspect.

Comparisons. The right and left lower premolars of *Gerhardodon purbeckensis* are identified as ?p3, as they do not bear buccal cusps (although buccal cusps are present in p3 of all adequately known Portuguese paulchoffatiids, personal communication from Professor Gerhard Hahn). This ?p3 is closer to p3 of the Paulchoffatoidea than Plagiaulacoidea in being roughly trapezoidal rather than triangular and short rather than tall. In most paulchoffatoid taxa (Hahn 1969, 1978*b*, 1978*c*, 1987) the upper margin of p3 has been abraded. It has been well preserved in *Kuehneodon uniradiculatus*

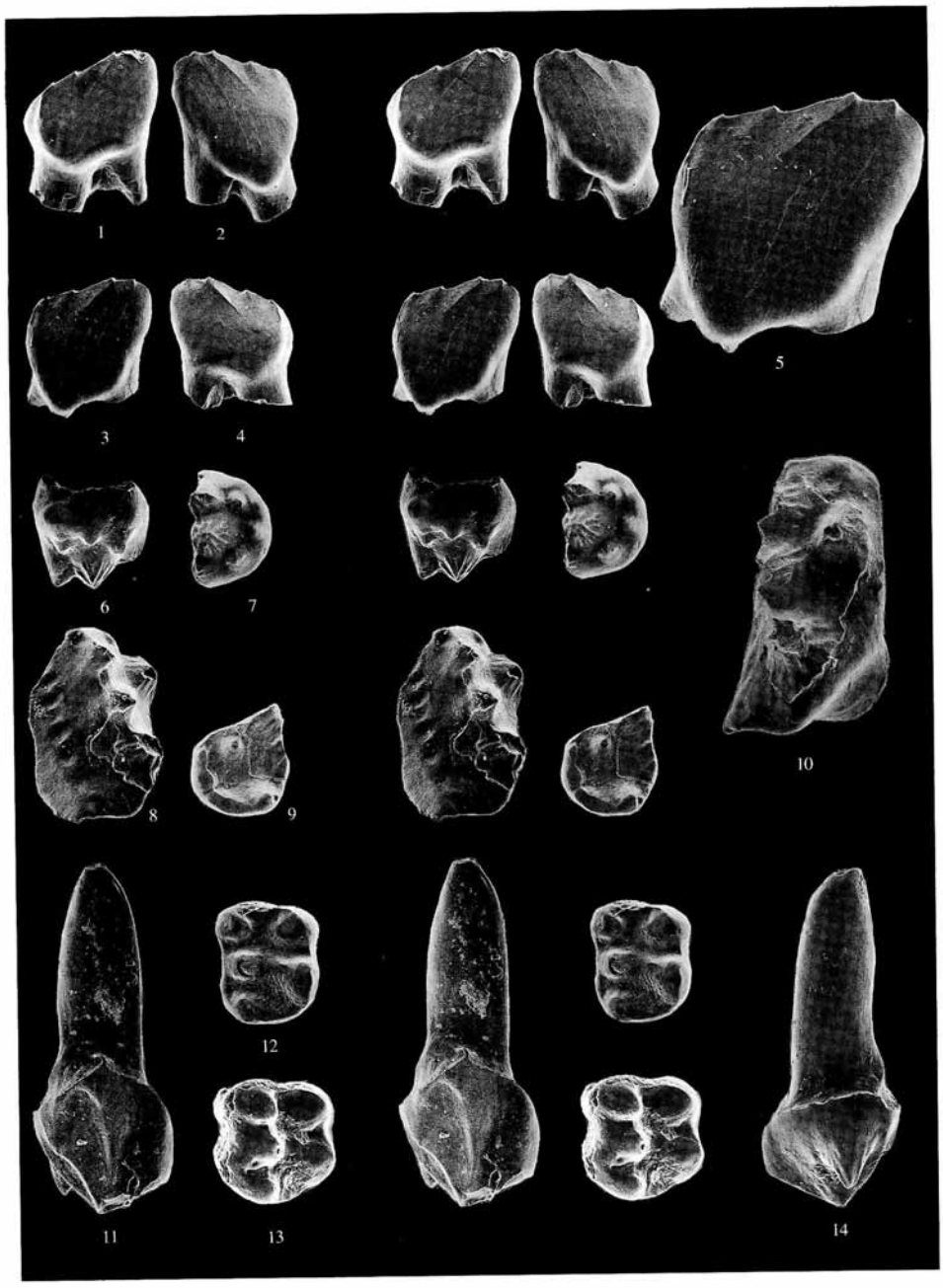
EXPLANATION OF PLATE 1

All specimens are from the Purbeck Limestone Formation, Cherty Freshwater Member. Specimen in figure 9 is from Suttle's Quarry near Swanage; all others are from Sunnydown Farm Quarry near Langton Matravers. All are scanning electron micrographs; figure 5 is ×40; all others ×20. Except where stated, all teeth in occlusal view are oriented with anterior margin up.

Figs 1–5. *Gerhardodon purbeckensis* sp. nov. 1–2, DORCM GS 20; right ?p3, lingual and buccal views. 3–5, DORCM GS 19; holotype; left ?p3, buccal, lingual and buccal views. All except figure 5 are stereo-pairs.

Figs 6–10, 12–13. cf. *Gerhardodon purbeckensis* sp. nov. 6–7, DORCM GS 21; anterior part of the ?right upper premolar, anterior and occlusal views (in figure 7 anterior margin is to the right). 8, 10, DORCM GS 11; left ?P5, occlusal and buccal views. 9, DORCM GS 15; anterior part of the right m1 (anterior margin downwards). 12–13, DORCM GS 9; left ?M1, occlusal and oblique lingual views. All except figure 10 are stereo-pairs.

Figs 11, 14. ?Plagiaulacinae, gen. et sp. indet. DORCM GS 14; left I3, posterior and anterior views; figure 11 is a stereo-pair.



KIELAN-JAWOROWSKA and ENSOM, *Gerhardodon*, ?Plagiaulacinae

(Hahn 1978*b*, text-fig. 9), in dp3 or *Kuehneodon dietrichi* (Hahn 1978*c*, text-fig. 1) in dp2–dp4 of Paulchoffatiidae gen. et sp. indet. (Hahn 1987, text-fig. 6), in *Guimarotodon leiriensis* (Hahn 1987, text-fig. 5) and dp3 of Paulchoffatiidae gen. et sp. indet. (Hahn 1987, text-fig. 6). In all these species p3, p4 and dp2, dp3 and dp4, when known, bear buccal cusps. It is not known whether *Paulchoffatia* had premolars with straight or slightly vaulted upper margins (Kühne 1961; Hahn 1969, 1978*b*). *Paulchoffatia* differs from other paulchoffatiid genera in having a large p2 similar to p3. It is possible that ?p3 of *G. purbeckensis* is p2 of *Paulchoffatia* type or even p4, which has lost the buccal cusps.

cf. *Gerhardodon purbeckensis* sp. nov.

Plate 1, figs 6–10, 12–13; Text-figs 5D, 6C

Material. Several isolated teeth in the collection from the Cherty Freshwater Member of the Purbeck Limestone Formation are similar to those of the Paulchoffatoidea, rather than Plagiaulacoidea. They fit the size of the lower premolars of *Gerhardodon purbeckensis* and may be conspecific with it. We assign them tentatively to *G. purbeckensis*. These are: DORCM GS 15 (sample 05) from Suttle's Quarry near Swanage, anterior part of the right m1, and three specimens from Sunnydown Farm Quarry near Langton Matravers: DORCM GS 21 (sample 95) anterior part of a ?right upper premolar; DORCM GS 11 (sample 4) left P4 or P5; DORCM GS 9 (sample 28), left ?M1.

Description. Right m1. DORCM GS 15 (Pl. 1, fig. 9) only the anterior part of the crown without roots has been preserved. Along the anterobuccal rim there are three cuspules, heavily worn in this specimen, the first of which is the largest and is transversely elongated. The next cuspule is smaller, the most posterior one is the smallest. Only the first (rounded) cusp of the buccal row has been preserved. This is situated opposite the third of the above described anterobuccal cuspules. On the anterolingual margin there is a rounded cusp, worn buccally, the worn surface being confluent with the worn surface of the first anterobuccal cuspule. There are two cusps in the lingual row. To the rear of the first lingual cusp the oblique ridges extend from the lingual margin towards the middle of the tooth.

Upper premolars. DORCM GS 21 (Pl. 1, figs 6–7), anterior part of the ?right upper premolar without roots; the preserved part is 0·9 mm wide. There are three small cuspules along the anterior margin, two main cusps (which may correspond to the anterior cusps of the middle and buccal rows, the middle being the larger) and possibly one more, smaller and broken lingual cusp. We recognize the rim with three cuspules as the anterior one by comparison with P5 of *Paulchoffatia delgadoi* (Hahn 1969) and *Henkelodon naias* (the latter referred to by Hahn 1977, text-fig. 10, as M1) and because this side bears a distinct oval facet (Pl. 1, fig. 6), suggesting the presence of a tooth in front of it. We believe that the tooth is the right one by comparison with *Henkelodon* and with left ?P4 or P5 (DORCM GS 11) described below. In both DORCM GS 21 and DORCM GS 11 there are three rows of cusps and the cusps in the lingual row are smaller than those in the middle row.

Left ?P4 or P5 (DORCM GS 11), (Pl. 1, figs 8, 10; Text-fig. 5D), has its roots broken off; it is 1·5 mm long and 0·9 mm wide; the tooth has a broken anterolingual corner and is badly damaged. The cusp formula is 1:3:?7. The row of lingual cusps is directed obliquely upwards when the middle row is placed horizontally. The tooth originally had a row of ?seven small lingual cusps, which are worn out and small oval transverse grooves are preserved between them. There are three large cusps in the middle row, the ultimate one being larger than the first two, which are strongly worn lingually. There is one large cusp in the buccal row, placed opposite the groove between the first and second cusps of the middle row. Along the anterior margin two worn cuspules are preserved, but as the anterolingual corner of the tooth is broken off, one can presume that there were originally three cuspules as in DORCM GS 21. The enamel is not preserved on the lingual part of the tooth; it is retained on the cusps of the middle row (although worn on the lingual side of the first two cusps) and on the buccal cusp. The cusps on which enamel is preserved are ornamented with radiating ridges. DORCM GS 11 and DORCM GS 21 because of the different state of preservation appear very different at first sight. However, in both teeth there are possibly three minute anterior cuspules, and three rows of cusps, the lingual being the smallest. DORCM GS 11 and GS 21 may either represent the same tooth, or one may be P4 and the other P5.

Left ?M1 (DORCM GS 9), (Pl. 1, figs 12–13; Text-fig. 6C), has the roots broken; it is 1 mm long lingually, 0·95 mm long buccally, and 0·85 mm wide. The tooth is roughly rectangular in occlusal view, has rounded angles, and a narrow rim around the first lingual cusp. The cusp formula is 2:3. All five cusps are of almost the same size; the posterior one in the lingual row is slightly smaller. The buccal cusps are worn lingually, the lingual ones subhorizontally. The lingual margin opposite the groove between the penultimate and ultimate

lingual cusps is slightly convex lingually, but an incipient lingual ridge, characteristic of M1 in the Plagiaulacidae, is not developed.

Comparisons. We identify the fragmentary tooth DORCM GS 15 as the first lower molar, because of its similarity to these teeth in the Paulchoffatiidae (Hahn 1987), characterized by a row of anterobuccal cuspules and large first buccal cusp. Its attribution to cf. *Gerhardodon purbeckensis* is entirely tentative, based on size only. The upper premolar DORCM GS 21 was found in the same sample as the holotype specimen (lower premolar) of *Gerhardodon purbeckensis*; as it fits the holotype specimen in size, it may belong to the same individual, and if so, the other upper premolar DORCM GS 11 may also belong to *G. purbeckensis*. These P4 or P5 are reminiscent of P4 and P5 of *Pseudobolodon oreas* (Hahn 1977; Text-fig. 2), and *Henkelodon naias* (Hahn 1977, text-fig. 10, identified by Hahn as P5 and M1), in having three rows of cusps, the single cusp and cuspules in the buccal row being situated anterobuccally. The lingual cusps of P4 in *P. oreas* and *H. naias* are worn, but there were possibly four in *P. oreas*, and as many as seven in cf. *G. purbeckensis*.

DORCM GS 9 is tentatively identified as M1, because like the M1 of *Henkelodon naias* (referred to by Hahn 1977, text-fig. 10, as M2) it has a rectangular shape, two parallel rows of cusps and a small lingual convexity in the posterior part of the lingual margin, which is not developed into a ridge as in the Plagiaulacidae. DORCM GS 9 may be shown to be a right m1 rather than left M1.

Genus SUNNYODON gen. nov.

Etymology. From the locality Sunnydown Farm and Greek *odous*, meaning tooth.

Diagnosis. The same as for the only known species *Sunnyodon notleyi* sp. nov.

Sunnyodon notleyi sp. nov.

Plate 5, figs 3, 10; Text-fig. 5F

Etymology. Named in honour of Mr and Mrs R. F. Notley, the owners of Sunnydown Farm Quarry.

Holotype. DORCM GS 18 (sample 011) right ?P5 (Pl. 5, figs 3, 10; Text-fig. 5F).

Type horizon and locality. Purbeck Limestone Formation, Cherty Freshwater Member, Lovell's Quarry near Langton Matravers.

Diagnosis. ?P5 resembles P5 and P4 of *Paulchoffatia*, *Kuehneodon* and *Kielanodon* in having only two rows of cusps, but differs in having two cusps of the buccal row arranged symmetrically in the middle of the tooth length, and only one anterior and one posterior buccal cuspule. Differs from all known paulchoffatiid taxa in the presence of an incipient lingual ridge, with a small cuspule. In number and arrangement of cusps it resembles *Kielanodon*, but differs from P4 and P5 of that genus in being narrower, roughly oval in shape, and in having differently arranged cusps in the buccal row. Cusp formula 2:4:ridge.

Description. The species to which ?P5 DORCM GS 18 belongs was very small. ?P5 is 0·94 mm long lingually, 0·87 mm long measured along the middle of the buccal row of cusps and 0·67 mm wide across the level of the lingual ridge. There are two cusps of subequal size in the buccal row and two cuspules, one situated anterolingually with regard to the first cusp and the other posterolingually to the second cusp. The four cusps in the lingual row increase in size posteriorly. There is a minute cuspule placed anteriolingually to the first lingual cusp. All the cusps and buccal cuspules are ornamented with radiating ridges. Opposite the furrow between the penultimate and ultimate lingual cusps there is an incipient lingual ridge with a small, pointed cuspule in the middle.

Comparisons. *Sunnyodon notleyi* resembles P4 and P5 of *Kielanodon hopsoni* (Hahn 1987, text-fig. 7) in having four lingual and two buccal cusps. Additional cuspules in the buccal row are arranged in *K. hopsoni* posterior to the buccal cusps, while in *S. notleyi* one is anterior and one is posterior. The unusual feature of this tooth is the presence of an incipient lingual posterior ridge with a single cuspule, a ridge similar to those in M1 in plagiaulacoids. However, we think that this tooth is P5 or P4, rather than M1 because of the conical shape of the cusps with radiating ridges, which are characteristic of the paulchoffatoid and plagiaulacoid upper premolars and not of the molars. An incipient third lingual ridge similar to that in M1 in plagiaulacoids has not been described as yet in paulchoffatoid and plagiaulacoid upper premolars, but in almost all previously known paulchoffatoid upper premolars with two rows of cusps, the lingual side has been abraded. DORCM GS 18 does not belong to *Gerhardodon purbeckensis*, as there are other, differently shaped and larger upper premolars in the studied collection that fit better the size of the holotype specimen of *G. purbeckensis*, and which we tentatively assign to that taxon (see also Comparisons under cf. *G. purbeckensis* above).

cf. *Sunnyodon notleyi* sp. nov.

Plate 5, figs 5–6; Text-fig. 5E

Material. DORCM GS 17 (sample 27), ?left P4 or P3 from Sunnydown Farm Quarry near Langton Matravers, Cherty Freshwater Member of the Purbeck Limestone Formation.

Description. ?Left P4 or P3 DORCM GS 17 is roughly oval, with an incurvature on the posterior margin. It is 0·78 mm long lingually, 0·67 mm buccally and 0·61 mm wide. It bears four cusps of subequal size, two in the buccal row and two in the lingual row, the two lingual being placed to the rear of the buccal ones. In addition there is one buccal cuspule placed on the buccal margin, between the two cusps, and one lingual cuspule placed in front of the first lingual cusp. All the cusps are ornamented with radiating ridges.

Comparisons. ?P4 or P3 (DORCM GS 17), was found in sample 27, which also yielded a large I2 (DORCM GS 10), described below as belonging to Plagiaulacinae gen. et sp. indet. a, I2. However, the two specimens from sample 27 differ markedly in size, which precludes their assignment to the same taxon. ?P5 (DORCM GS 18) and ?P4 or P3 (DORCM GS 17) may belong to the same species as they fit each other in size and are the only upper teeth of this size in the studied collection. ?P4 or P3 (DORCM GS 17), which we tentatively assign to *Sunnyodon notleyi*, has four cusps and additional cuspules and is of paulchoffatoid rather than plagiaulacoid pattern. Of the known paulchoffatoid taxa it resembles possibly most the P3 of *Kielanodon hopsoni* (Hahn 1987, text-figs 7–8), with four cusps, from which it differs in being more regularly oval and in having only two cusps and one cuspule in the lingual row.

Remarks on paulchoffatoid taxa from the Purbeck Limestone Formation of England

The multituberculates previously described from the Purbeck Limestone Formation of England (Falconer 1857, 1862; Owen 1854, 1871; Simpson 1928) are, in our opinion, members of the Plagiaulacoidea, although Hahn and Hahn (1983) assigned *Bolodon* and *Plioprion* to the Paulchoffatiidae (see 'Remarks' under Plagiaulacidae below). In the collection from the Cherty Freshwater Member of the Purbeck Limestone Formation described in this paper, in addition to members of the Plagiaulacidae that prevail, there are teeth which we assign to the Paulchoffatiidae. We believe that there are at least two paulchoffatoid taxa in the collection studied, a slightly larger one, *Gerhardodon purbeckensis*, and a very tiny one, *Sunnyodon notleyi*.

The holotype specimens of these two taxa and other teeth tentatively assigned to them show a mixture of characters that may be found in almost all paulchoffatoid genera known from the Kimmeridgian or Oxfordian (Helmdach 1971; Mohr 1989) of Portugal, assigned either to the Paulchoffatiinae or to the Kuehneodontinae. Therefore we leave *Gerhardodon* gen. nov. and *Sunnyodon* gen. nov. for the time being in subfamily *incertae sedis*; we cannot rule out that they belong to different subfamilies.

Suborder PLAGIAULACOIDEA (Simpson, 1925), Hahn, 1969
Family PLAGIAULACIDAE Gill, 1872
Subfamily PLAGIAULACINAE Gill, 1872

Remarks. Hahn (1969) divided the Plagiaulacoidea into the Paulchoffatiidae Hahn, 1969 and Plagiaulacidae Gill, 1872 (see also Hahn 1971, 1977, 1978*b*, and Hahn and Hahn 1983), the families which we now regard as belonging to separate suborders. Important differences according to Hahn and Hahn (1983, p. 58) are: the structure of m2 which in the Paulchoffatiidae is 'Becken-förmig gebaut, mit erhöten, umlaufendem Rand und nur einen, antero-lingual gestallten Höcker', while in the Plagiaulacidae is (p. 81): 'm2 gebaut wie m1, mit 2 Längs-Reichen von Höckern'; and the structure of I3 which in the Paulchoffatiidae is three-cusped, and two-cusped in the Plagiaulacidae, similar to I2 (but see Diagnoses of suprageneric taxa above). The bulk of the paulchoffatoid genera come from the Kimmeridgian or Oxfordian (Helmdach 1971; Mohr 1989) of Guimarota in Portugal. Hahn and Hahn (1983) assigned to the Paulchoffatiidae, among others, two genera from the Purbeck Limestone Formation of England: *Bolodon* Owen, 1871, based on upper jaws, and *Plioprion* Cope, 1884, based on lower jaws (regarded by us as congeneric). In the material described in this paper seven isolated teeth that we regard as belonging to the same individual were found in sample 61. The M2 found in this sample (Pl. 3, figs 7–8) does not differ at the specific level from that in the holotype specimen of *Bolodon osborni* Simpson (BMNH 47735A, Pl. 3, fig. 9). The lower premolars from the same sample (Pl. 2, figs 4–6) are conspecific with those of *Ctenacodon* cf. *minor* (Falconer) (Simpson 1928, p. 40; see also Pl. 2, figs 3, 7), assigned by Hahn and Hahn (1983) to *Plioprion* Cope. On this basis we regard *Plioprion* cf. *minor* (Falconer) as a junior synonym of *Bolodon osborni* Simpson, and *Plioprion* Cope, 1864 a junior synonym of *Bolodon* Owen, 1871. We assign *Bolodon* Owen to the Plagiaulacinae in Plagiaulacidae (contra Hahn 1969 and Hahn and Hahn 1983) for the following reasons: The crowns in p2 and p3 in *Bolodon* are triangular and tall as characteristic of the Plagiaulacoidea, while in the Paulchoffatoidea the crowns in p2 and p3 are lower, oval or roughly quadrangular. p4 in *Bolodon* is elongated longitudinally, about twice as long as p3 (as characteristic of the Plagiaulacidae), while in the Paulchoffatiidae p4 is as long as p3. Other reasons for assigning *Bolodon* to the Plagiaulacidae are the structure of M2 and m2. In the Plagiaulacidae M2 has the cusp formula 2–3:3 and differs in this respect from that in the Paulchoffatiidae where the cusp formula of M2 is 2–3:3–6 (Hahn 1969, 1971). In m2 of *Bolodon* (Text-fig. 4) and possibly *Plagiaulax* (the only known m2 of the latter, BMNH 47733 is heavily worn, see Falconer 1857, figs 7–10 and Kielan-Jaworowska *et al.* 1987, pl. 8, fig. 1), there are no discrete buccal cusps but only a rounded ridge. m2 in *Bolodon* is reminiscent of those in the Paulchoffatiidae (e.g. Hahn 1969, figs 36–38; 1971, fig. 19; Text-fig. 4B, D) in having a buccal ridge instead of discrete cusps, but differs in having a longitudinal middle groove and two lingual cusps (whereas there is only one in the Paulchoffatiidae). The only known m2 of *Bolodon* is that of *Bolodon minor* (BMNH 47729), now lost (figured by Falconer 1854, fig. 15, and Owen 1871, pl. 4, fig. 9B, as *Plagiaulax minor*). The wear of the specimen and possible inadequacy of the drawings induced Hahn (1969) to believe that this m2 had a structure characteristic of the Paulchoffatiidae. As shown by the well preserved m2 of *Bolodon osborni* (Pl. 3, figs 5–6; Text-fig. 4B), m2 in *Bolodon* differs from that in the Paulchoffatiidae in having a longitudinal groove and two cusps in the lingual row, and from the Allodontidae in the lack of discrete buccal cusps.

Genus BOLODON Owen, 1871

Synonym. *Plioprion* Cope, 1884.

Type species. *Bolodon crassidens* Owen, 1871.

Revised diagnosis. Dental formula: 3,0,5,2/1,0,4,2. Smallest plagiaulacine genus that differs from *Plagiaulax* in having smaller lower incisor and four lower premolars rather than three (both shared

with '*Bolodon*' *falconeri*). Differs from *Plagiaulax* and '*Bolodon*' *falconeri* in having smaller number of buccal cusps in p4 (1–?4) rather than ?6. Differs from '*Bolodon*' *elongatus* in having P1–P3 without prominent posterior cingulum and P1 of subequal size with P2 rather than distinctly larger.

Species. B. crassidens, *B. osborni* and *B. minor*. '*Bolodon*' *falconeri* and '*Bolodon*' *elongatus* possibly do not belong to this genus.

Remarks. P4–M2 and m1–m2, well-preserved in *Bolodon* species, are unknown or badly damaged in other plagiaulacine genera and cannot be compared. See also the diagnosis of Plagiaulacinae under 'Diagnoses of suprageneric taxa' above.

Bolodon osborni Simpson, 1928

Plate 2, figs 3–7; Plate 3, figs 3–9; Plate 4, figs 3–7, 9–11; Plate 5, fig. 4; Text-figs 3C, 4B, 5B, 6A

1928 *Bolodon osborni* sp. nov. Simpson, p. 45, pl. 3, fig. 6; text-fig. 10.
1928 *Ctenacodon ?minor* Falconer, Simpson, p. 40, pl. 3, fig. 5.
1971 *Bolodon osborni* Simpson; Hahn, text-fig. 14.
1987 *Bolodon osborni* Simpson; Kielan-Jaworowska, Dashzeveg and Trofimov, pl. 10, fig. 3; text-fig. 3A.

Holotype. BMNH 47735A right maxilla with P1, P3–M2, figured by Simpson (1928, pl. 3, fig. 6, text-fig. 10); by Hahn (1971, text-fig. 14); Kielan-Jaworowska *et al.* (1987, pl. 10, fig. 3); and Pl. 3, fig. 9; Pl. 4, figs 9, 11; Pl. 5, fig. 4 in this paper.

Type horizon and locality. Purbeck Limestone Formation, Marly Freshwater Member, Durlston Bay, Swanage.

Other material. BMNH 48399 right dentary from the type horizon and locality, with p1–p4 exposed in lingual aspect (figured by Simpson, 1928, pl. 3, fig. 5, as *Ctenacodon* cf. *minor*, and erroneously referred to in the explanation to the plate as the buccal aspect of the left dentary; Pl. 2, fig. 7) and left p4 registered under the same number, possibly belonging to the same specimen (Pl. 2, fig. 3). The remainder of the material is from the Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers, Swanage, Dorset. These are: seven teeth found in sample 61, all left, fitting each other in size and regarded as belonging to the same individual: all in DORCM GS 204, p2; GS 202, p3; GS 201, p4; GS 203, m1; GS 206, m2; GS 207, M2; GS 205 broken I2; GS 4, left m1 (sample 3); GS 1, P2 or P3 (sample 35); GS 3, P2 or P3 (Bulge sample); GS 5, P2 or P3 (Bulge sample).

Diagnosis. Shares with *B. minor* 6–7 serrations in p4, but differs from it in being larger (p4 being 2·4–2·7 mm long), in having only a single buccal cusp in p4, ridges on p4 more widely spaced and

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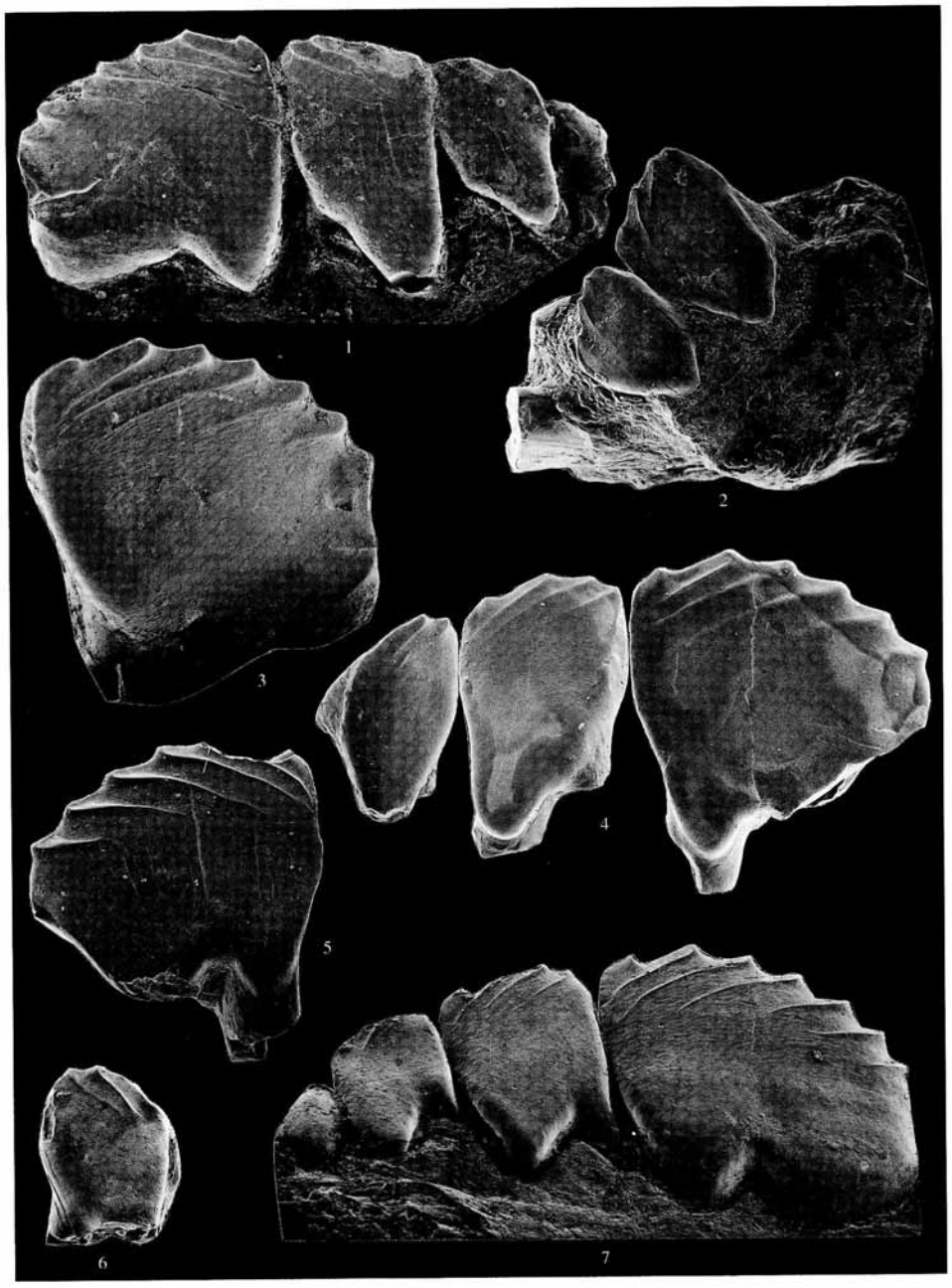
EXPLANATION OF PLATE 2

All from the Purbeck Limestone Formation. Specimens in figures 1, 3 and 7 are from the Marly Freshwater Member, Durlston Bay, Swanage; specimens in figures 2, 4–6, are from the Cherty Freshwater Member; specimen in figure 2 is from Suttle's Quarry near Swanage; specimens in figures 4–6 from Sunnydown Farm Quarry near Langton Matravers. All are scanning electron micrographs, ×20.

Figs 1–2. *Bolodon minor* (Falconer). 1, BMNH 47729; epoxy resin cast of the holotype; fragment of the right mandible with p1–p4, buccal view. 2, DORCM GS 12; fragment of the left mandible with broken incisor; p2 and p3, buccal view.

Figs 3–7. *Bolodon osborni* Simpson. 3, BMNH 48399; epoxy resin cast of left p4, buccal view. 4, photomontage of three teeth from the same sample: DORCM GS 204, p2; DORCM GS 202, p3; DORCM GS 201, p4, buccal view. 5, DORCM GS 201; p4, lingual view, part of the upper margin has been broken after the photograph in figure 4 was taken. 6, DORCM GS 204; p2, lingual view. 7, BMNH 48399; epoxy resin cast; right mandible with p1, p2, p3 and p4, lingual view.



KIELAN-JAWOROWSKA and ENSOM, *Bolodon*

p3 relatively larger in relation to p4. Differs from *B. crassidens* in being smaller, in having P4 more parallel-sided with three large cusps in the middle row, a cuspule in front of them and a row of buccal cuspules, rather than two large middle cusps, and a smooth prominent anterobuccal cingulum.

Description. Estimated length of the skull is about 3 cm.

Lower teeth. The lower incisor has not been preserved. p1 is preserved only in BMNH 48399 and is exposed in lingual aspect (pl. 2, fig. 7). p2–p4 from Sunnydown Farm Quarry are shown in pl. 2, figs. 4–6; p2 (DORCM GS 204) has one weak and two distinct serrations, two ridges on the buccal side and three on the lingual side; it is 1·7 mm long and 0·8 mm wide. p3 (DORCM GS 202) is 2·1 mm long and 1·1 mm wide, it has four serrations and all except the first one bear ridges. In buccal aspect a short ridge extends downward from the last serration and there is a minute cuspule below it. The ventral margin of the exodaenodont lobe is very prominent. p4 (DORCM GS 201) is 2·4 mm long and 2·3 mm high and has six serrations, all except the first one provided with ridges. This specimen is incomplete, and the posteroventral part, posterior root and buccal cusp have not been preserved. A single buccal cusp is preserved in the left tooth of BMNH 48399 (Pl. 2, fig. 3). The cusp formula of m1 is 2:2. The tooth is roughly rectangular, but slightly shorter lingually than buccally. m1 (DORCM GS 203) is 1·4 mm long and 1·2 mm wide, while DORCM GS 4 is 1·5 mm long and 1·2 mm wide (Pl. 3, figs 3–4). In DORCM GS 203 the large posterior root is almost completely preserved, the anterior one is broken at the base; in DORCM GS 4 both roots are broken, a small part of the posterior one being preserved. Both cusps in the lingual row are crescent-shaped, with large, roughly triangular surfaces sloping towards the middle groove. In DORCM GS 4 on the first lingual cusp, in front of the main cusp, there is a minute cuspule, which is less prominent in GS 203 because of wear. Both cusps of the lingual row, as preserved in both specimens, are not ornamented. In the buccal row there is an elevated cingulum in front of the first cusp. The first cusp is roughly cone-shaped, with four surfaces sloping down from the tip, the posterior one ornamented with grooves. The second cusp has its tip situated buccally, worn in both specimens and a large crescentic surface, strongly ornamented with irregular grooves, that slopes down anterolingually from the tip. m2 DORCM GS 206 (Pl. 3, figs 5–6) is 1·6 mm long and 1·3 mm wide, roughly oval, with slightly sigmoid anterior margin. Both roots are broken off. The first cusp of the lingual row as preserved in DORCM GS 206 is not ornamented and has three surfaces that slope down from the tip: a crescent-shaped anterolingual, and two roughly triangular buccal and posterior ones. A wide groove divides the two cusps of the lingual row. The second lingual cusp is elongated longitudinally, roughly triangular in occlusal aspect, with the tip situated in the anterior one third of the length. A ridge extends from the tip posteriorly, separating the buccal and lingual slopes. The anterior slope is irregular, ornamented with a crescent-shaped, prominent ridge. The buccal slope was originally ornamented with grooves and ridges; only the first ridge is well preserved. The buccal side forms a prominent rounded ridge, with traces of three minute cuspules in the posterior half. A large surface, conspicuously ornamented with irregular, mostly transverse grooves and ridges, slopes down from the rounded ridge to the middle groove. The anterior part of the buccal ridge is worn.

Upper teeth. I1, I3 and P2 are not known. I2 (DORCM GS 205: Pl. 4, fig. 3) is a fragment of the left tooth with broken tip and part of the accessory cusp preserved. It is similar to I2 DORCM GS 8 (Pl. 4, fig. 1) described under Plagiaulacinae gen. et sp. indet. a, I2, but is notably smaller. P1, P4, P5 and M1 have been preserved only in the holotype specimen (Pl. 4, figs 9, 11). P3 in the holotype specimen is partly obscured by P4. We identify three specimens (DORCM GS 1, GS 3 and GS 5) as P2 or P3 (Pl. 4, figs 4–7, 10), because they are all two-rooted, although the roots have been broken, and because they roughly correspond in size and

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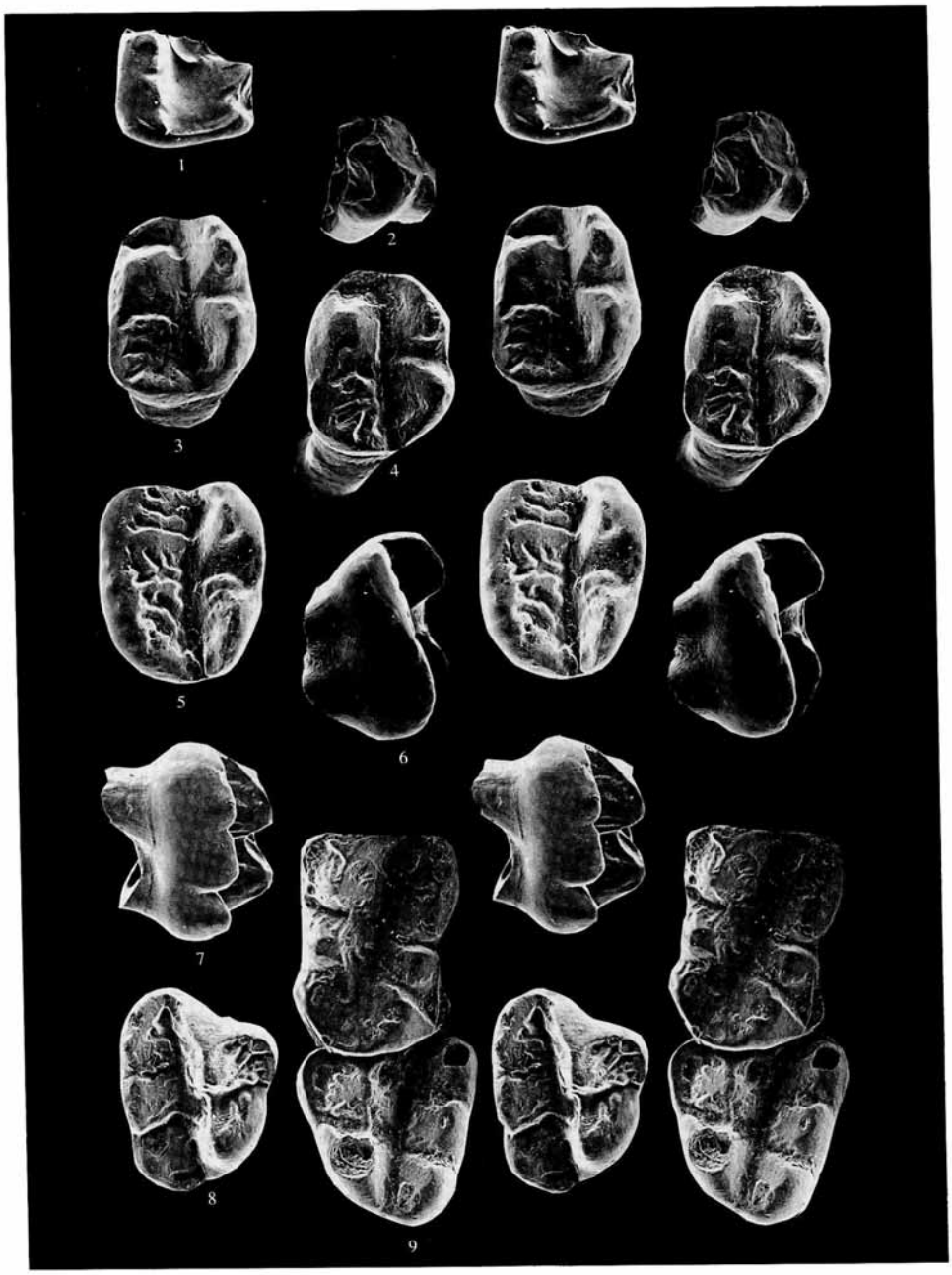
EXPLANATION OF PLATE 3

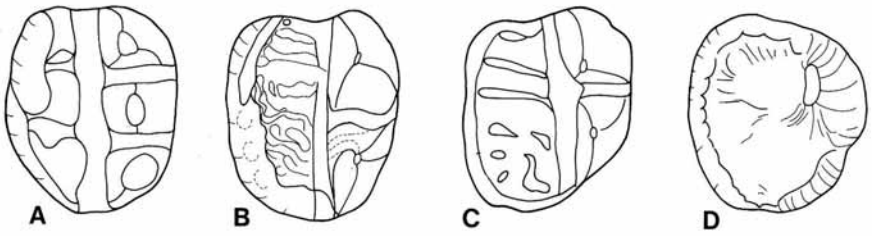
All are from the Purbeck Limestone Formation. Specimens in figures 1–8 are from the Cherty Freshwater Member, Sunnydown Farm Quarry, Langton Matravers. Specimen in figure 9 is from the Marly Freshwater Member, Durlston Bay, near Purbeck, Swanage. All are scanning electron stereo-micrographs ×20. All teeth are oriented with anterior margin up.

Figs 1–2. cf. *Bolodon minor* (Falconer). DORCM GS 6; posterior part of the right M1, occlusal and lingual views.

Figs 3–9. *Bolodon osborni* Simpson. 3, DORCM GS 4; left m1, occlusal view. 4, DORCM GS 203; left m1, occlusal view. 5–6, DORCM GS 206; left m2, occlusal view and buccal views. 7–8, DORCM GS 207; left M2, lingual and occlusal views. 9, BMNH 47735A; right M1 and M2, occlusal view.



KIELAN-JAWOROWSKA and ENSOM, *Bolodon*



TEXT-FIG. 4. Comparison of the left second lower molars, occlusal views. A, *Ctenacodon scindens* YPM 10366; right tooth, reversed. B, *Bolodon osborni*; DORCM GS 206. C, *Eobaatar magnus*; PIN 3101/53. D, Paulchoffatiidae, gen. et sp. indet. A–C are camera lucida drawings; A, of epoxy resin cast; B–C of original specimens; D is after Hahn 1969, text-fig. 36*a*, simplified. Scale = 1 mm.

structure to P3 in the holotype, while P2 has not been preserved in the holotype. The posterior cingulum obscured in P3 in the holotype, is well seen in all of them. They are all smaller than P1 of the holotype (Pl. 4, fig. 11) and differ from it in absence of the anterior cingulum.

M2 (DORCM GS 207) (Pl. 3, figs 7–8) appears on the photograph in occlusal view narrower than the holotype specimen (Pl. 3, fig. 9), which is in part due to a slightly different position on the photographed specimens, and possibly has a more sigmoid anterior margin. It is notably longer lingually than labially, divided by a deep longitudinal groove. There is a narrow anterior rim that widens medially and passes onto the first cusp of the buccal row, reaching its tip. The rim protrudes laterally and surrounds the base of the first buccal cusp, which is very irregular in shape. Its tip, as preserved in DORCM GS 207, forms a longitudinal ridge. Four surfaces slope up from the ridge: the anterior one is smooth and forms a part of the anterior rim mentioned above; the buccal one is the largest and surrounded by a rim; the posterior one is steep and small; the lingual one is steep and large; it protrudes anteriorly and reaches the anterior rim. The second cusp of the buccal row is roughly triangular. Three surfaces slope up from its tip: the anterior one is roughly triangular, the posterobuccal is crescent-shaped and convex, and the lingual one is steep. In lateral view the buccal cusps coalesce at the bases. The first cusp in the lingual row has its tip placed posteriorly. Three surfaces slope up from it: the large buccal one which reaches the longitudinal groove; the anterolingual one, which is convex and crescent-shaped, and a very small posterior one. The second cusp is the shortest in the row. Due to wear the tip in DORCM GS 207 has the form of a ridge. There is a large, flat buccal slope and a convex lingual one. Anterior and posterior slopes are hardly pronounced. The third cusp is roughly a mirror-image of the first one, but has its tip situated in the middle. Except for the outer wall all the cusps of the tooth are ornamented with prominent pits and grooves. The grooves on the buccal slopes of the lingual cusps continue onto the lingual

EXPLANATION OF PLATE 4

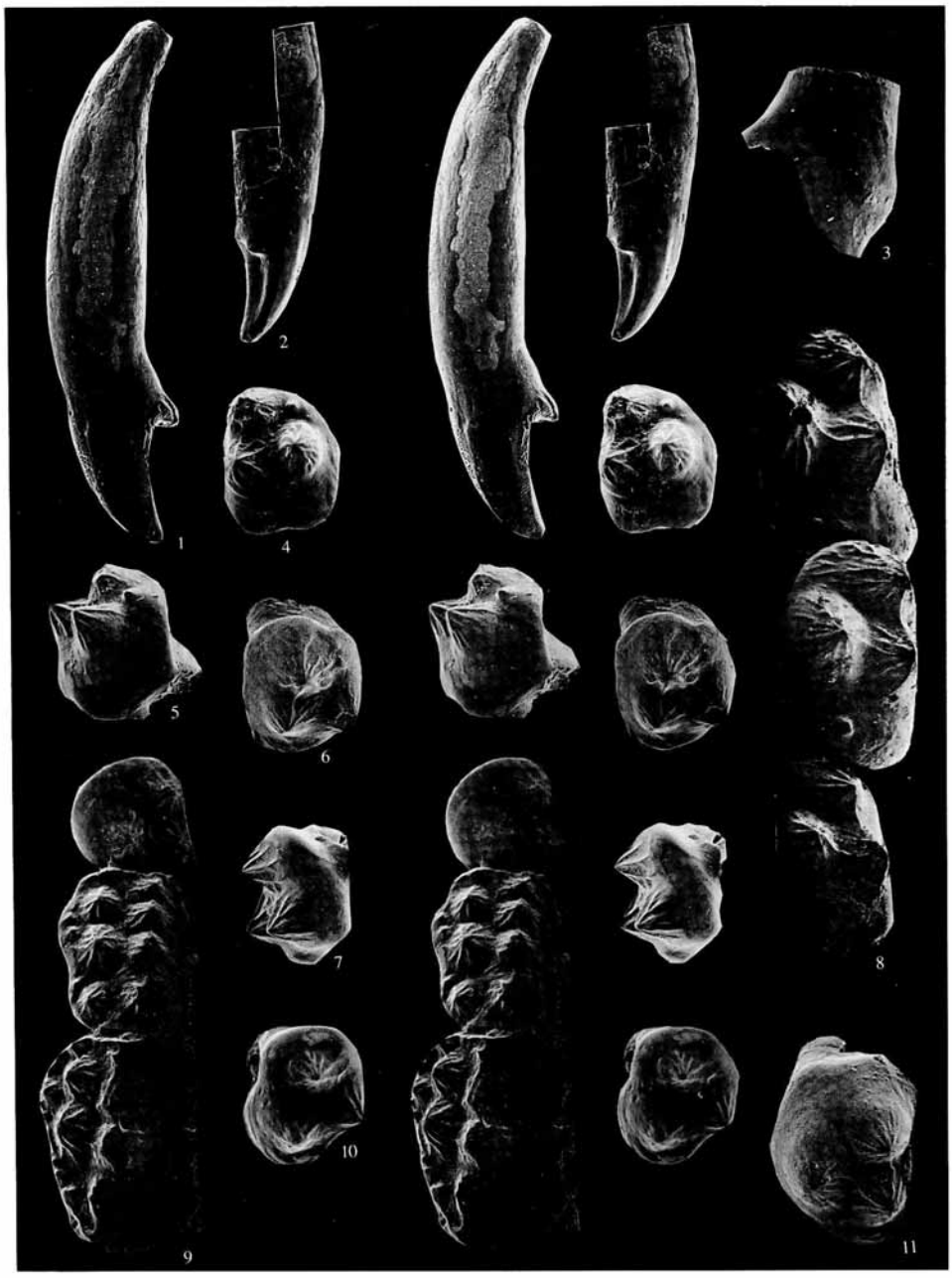
All are from the Purbeck Limestone Formation, specimens in figures 1–7 and 10 are from the Cherty Freshwater Member, Sunnydown Farm Quarry near Langton Matravers, specimens in figures 8–9 and 11 are from the Marly Freshwater Member, Durlston Bay, Swanage. All are scanning electron micrographs; figures 1–2 × 10, all others × 20. All except 3, 8 and 11 are stereo-pairs. All teeth in occlusal view are oriented with anterior margin up.

Fig. 1. Plagiaulacinae gen. et sp. indet. a. DORCM GS 8; right I2, lingual view.

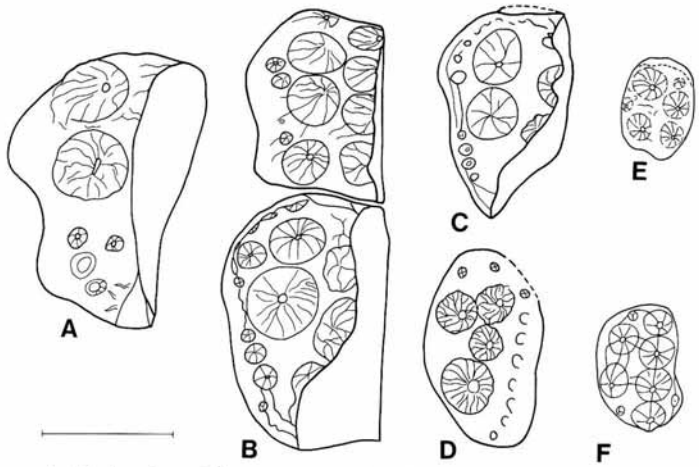
Fig. 2. Plagiaulacinae gen. et sp. indet. b. DORCM GS 10; left I2, lingual view.

Figs 3–7, 9–11. *Bolodon osborni* Simpson. 3, DORCM GS 205; broken left I2, lingual view. 4–5, DORCM GS 1; left P2 or P3, occlusal and buccal views. 6, DORCM GS 3; left P2 or P3, occlusal, slightly anterior view. 7, 10, DORCM GS 5; left P2 or P3, buccal and occlusal views. 9, 11, BMNH 47735A; 9, right P3–P5 occlusal view; 11, right P1, occlusal and slightly anterior view.

Fig. 8. '*Bolodon*' *elongatus* Simpson. BMNH 47736; fragment of right maxilla with P1–P3 of the holotype specimen, epoxy resin cast, occlusai view.



KIELAN-JAWOROWSKA and ENSOM, Plagiaulacinae, *Bolodon*



TEXT-FIG. 5. Camera lucida drawings of the upper premolars, in occlusal view. A–C, are based on epoxy resin casts, all shown as right teeth, D–E reversed. A, *Bolodon crassidens*; BMNH 47735; P4. B, *Bolodon osborni*; BMNH 47735A; P4 and P5. C, cf. *Bolodon minor*; DORCM GS 7; P5. D, cf. *Gerhardodon purbeckensis*; DORCM GS 11; P5. E, cf. *Sunnyodon notleyi*; DORCM GS 17; ?P4 or P3. F, *Sunnyodon notleyi*; DORCM GS 18; ?P5. Scale = 1 mm.

slopes of the buccal cusps. The most prominent ornamentation is on the buccal slope of the first buccal cusp, where in addition to the pits and grooves there occur prominent ridges.

Variability. The specimens assigned here to *Bolodon osborni* differ slightly in size. In BMNH 48399 p4 is 2·7 mm long (left tooth), and 2·5 mm wide (right tooth, measured in lingual aspect), while p4 DORCM GS 201 is 2·4 mm long. M2 in the holotype specimen is slightly larger than DORCM GS 207. These differences are not greater than those observed in other multituberculate genera and species (see, e.g., Krause 1977, 1982, 1987; Kielan-Jaworowska *et al.* 1987).

EXPLANATION OF PLATE 5

All are from the Purbeck Limestone Formation, specimens in figures 1–3, 5–6 and 8–10 are from the Cherty Freshwater Member, specimens in figures 4 and 7 are from the Marly Freshwater Member. All are scanning electron micrographs, all except figures 4 and 7 are stereo-pairs. Figures 1–2, 4, 7–9, ×20; figures 3, 5–6, 10, ×40. All teeth are oriented with anterior margin up.

Figs 1–2. ?Plagiaulacinae, gen. et sp. indet. DORCM GS 2; Sunnydown Farm Quarry near Langton Matravers; ?right P1, P2 or P3, or left canine, occlusal and lingual views.

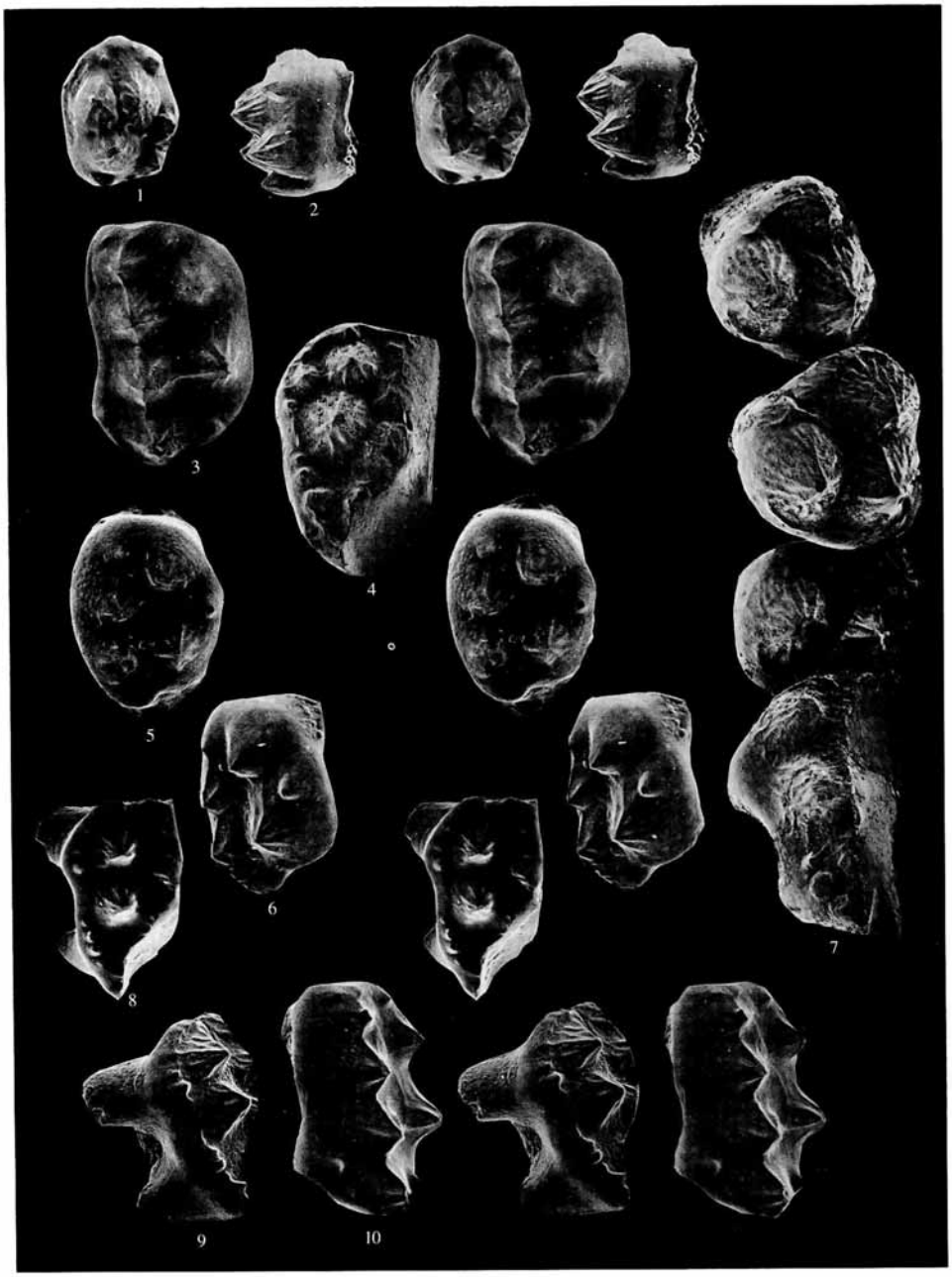
Figs 3, 10. *Sunnyodon notleyi* sp. nov. DORCM GS 18; holotype; Lovell's Quarry near Langton Matravers; right ?P5, occlusal and lingual views.

Fig. 4. *Bolodon osborni* Simpson. BMNH 47735A; epoxy resin cast of the right P5 of the holotype specimen; Durlston Bay, Swanage; occlusal view.

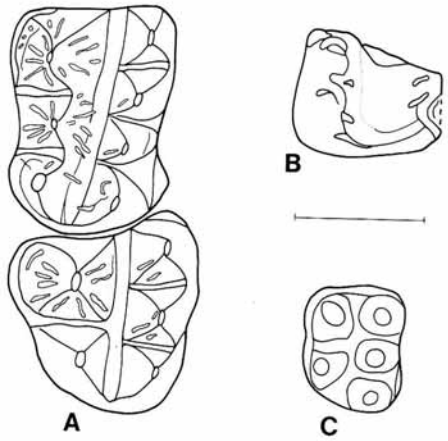
Figs 5–6. cf. *Sunnyodon notleyi* sp. nov. DORCM GS 17; Sunnydown Farm Quarry near Langton Matravers; ? left P3, occlusal and buccal views.

Fig. 7. *Bolodon crassidens* Owen. BMNH 47735; Durlston Bay, Swanage; epoxy resin cast of the fragment of maxilla with P1–P4 of the holotype specimen.

Figs 8–9. cf. *Bolodon minor* (Falconer). DORCM GS 7; Sunnydown Farm Quarry near Langton Matravers; right P5, occlusal and buccal views.



KIELAN-JAWOROWSKA and ENSOM, multituberculate mammals



TEXT-FIG. 6. Camera lucida drawings of the upper molars, occlusal view, all shown as right teeth. C–D reversed, A, based on epoxy resin cast. A, *Bolodon osborni*; BMNH 47735A; M1 and M2; M1 which slightly covers M2 in the specimen has been separated in the drawing. B, cf. *Bolodon minor*; DORCM GS 6; posterior part of M1. C, cf. *Gerhardodon purbeckensis*; DORCM GS 9; ?M1. Scale = 1 mm.

Comparisons. See 'Comparison of Plagiaulacinae species' below.

Bolodon minor (Falconer, 1857)

Plate 2, figs 1–2; Text-fig. 3B

1857 *Plagiaulax minor* sp. nov.; Falconer, pp. 262–267, 271–272, text-fig. 15 *a-d*.
1983 *Plioprion minor* (Falconer); Hahn and Hahn, p. 66, with synonymy, excluding *Ctenacodon* cf. *minor* Simpson 1928.
1987 *Plioprion*? *minor* (Falconer); Kielan-Jaworowska, Dashzeveg and Trofimov, pl. 10, fig. 3.

Holotype. BMNH 47729, right dentary with incisor, p1–m2 (m2 now lost), figured by Falconer 1857, pl. 3, fig. 15; Owen 1871, pl. 4, fig. 9; Simpson 1928, pl. 3, fig. 4, text-fig. 9; Hahn 1971, text-fig. 2; Kielan-Jaworowska *et al*. 1987, pl. 10, fig. 3, and this paper: Pl. 2, figs 1–2; Text-fig. 3B.

Type horizon and locality. Purbeck Limestone Formation, Marly Freshwater Member, Durlston Bay, Swanage.

Other material. DORCM GS 12 (sample 05) from Suttle's Quarry, Cherty Freshwater Member of the Purbeck Limestone Formation, a fragment of left dentary with broken incisor, p2 and p3; see also P5 and M1 described under cf. *Bolodon minor* below.

Diagnosis. Differs from *B. osborni* and *B. crassidens* in being smaller, the length of p4 being 2·1 mm. Differs from *B. osborni* in having ?four buccal cusps in p4 and the ridges more closely spaced.

Description. See Simpson (1928, p. 38). The lower incisor fragment preserved in DORCM GS 12 is strongly compressed laterally and covered with a thin layer of enamel. p2 and p3 preserved in the same specimen are 1·3 and 1·65 mm high respectively, lower than in the holotype where they are 1·5 and 2·2 mm high.

Comparisons. See 'Comparison of Plagiaulacinae species' below.

cf. *Bolodon minor* (Falconer, 1857)

Plate 3, figs 1–2; Plate 5, figs 8–9; Text-figs 5C, 6B

Material. In the collection from Sunnydown Farm Quarry there are two isolated teeth, right P5 DORCM GS 7 (sample 35) and posterior part of right M1 DORCM GS 6 (sample 35), which belong to *Bolodon*, but are smaller than *B. osborni* and differ from it in details. They apparently belong to *B. minor*.

Description. Right P5 DORCM GS 7 (Pl. 5, figs 8–9; Text-fig. 5c) has both roots broken off and is partly worn. It is 3·25 mm long and 2·2 mm wide. The cusp formula is 2:3. The cusps of the lingual row are strongly worn lingually. The middle cusp is the largest. The cusps of the buccal row are of subequal size and larger than those of the lingual row. The tip of the anterior lingual cusp is placed posteriorly. The tooth is surrounded anteriorly and buccally by a cingulum with small cuspules. Anteriorly the cuspules are developed only as small crenulations. Buccally, opposite the first buccal cusp there are three cuspules, the posterior one being the largest; to the rear of the second buccal cusp there are four cuspules, the penultimate being the largest. The worn lingual surface forms a large vertical wall, which swings buccally opposite the second buccal cusp, producing the pointed end of the tooth crown when seen in dorsal view. All of the cusps are ornamented with radiating striae. The partial right M1 DORCM GS 6 (Pl. 3, figs 1–2; Text-fig. 6B) is possibly somewhat smaller than in *B. osborni*. It has an almost straight posterior margin, rather than convex as in *B. osborni* (pl. 3, fig. 9). A ridge, parallel to the posterior margin extends between the posterior cusps of the buccal and lingual rows. In the preserved fragment, which may represent half of the tooth, there are three small buccal cusps, which suggests that the number of buccal cusps was possibly greater than in *B. osborni*. Two strongly worn lingual cusps are preserved with traces of comma-shaped grooves, characteristic of the molars of *Bolodon*. The crescent-shaped lingual ridge characteristic of *B. osborni* has not been preserved.

Comparisons. See 'Comparison of Plagiaulacinae species' below.

Plagiaulacinae gen. et sp. indet. a, I2

Plate 4, fig. 1

Material. DORCM GS 8 (sample 112), right I2 from Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers.

Description. I2 (DORCM GS 8) is 8·5 mm long with root, strongly bent anteriorly, flattened laterally and provided with a prominent accessory cusp. The root is closed. The distance between the tips of the main and accessory cusps is 2 mm. The tooth is slightly constricted above the accessory cusp and its width at that point is 1·5 mm, but otherwise the crown gradually passes into the root. The posterior surface of the main cusp is strongly worn.

Comparisons. I2 (DORCM GS 8) is about 1·6 times larger than the fragmentary I2 (DORCM GS 205) (Pl. 4, fig. 3) assigned to *B. osborni*. It may belong to one of the two large plagiaulacine species based on the lower jaws: *Plagiaulax becklesii* or '*Bolodon*' *falconeri* in both of which p4 is about 1·6 times longer than in *Bolodon osborni* (BM 47729). One of these taxa is possibly a counterpart of '*Bolodon*' *crassidens*, while the other is a counterpart of '*Bolodon*' *elongatus*. I2 (DORCM GS 8) is smaller and more bent than I2 in *Psalodon fortis* and has a more prominent accessory cusp (Simpson 1929, p. 26, pl. 5, fig. 3). It differs from I2 in Paulchoffatiidae (e.g. *Kuehneodon dryas*, *K. simpsoni* and *Henkelodon naias*, see Hahn 1977) in being more bent, relatively slender, with a less robust accessory cusp and less prominent difference of the diameter between the crown and the root.

Plagiaulacinae gen. et sp. indet. b, I2

Plate 4, fig. 2

Material. DORCM GS 10 (sample 27), left I2 from Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers.

Description. DORCM GS 10 has a complete crown and part of the root preserved. It gradually diminishes in diameter towards the main cusp. At about 0·7 mm from the tip of the main cusp, there is an angulation with a minute lingual accessory cuspule.

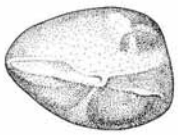
Comparisons. I1 in the Plagiaulacidae except for the alveoli and roots has not been described, but the root of I1 preserved in the type skull of *Bolodon crassidens* is very small, much smaller than that

of I2; it therefore seems improbable that DORCM GS 10 is an I1. Among the Paulchoffatiidae Hahn (1969, 1977) described I1 in *Paulchoffatia delgadoi*, *Paulchoffatia* sp. (referred to as *Kuehneodon* sp., Hahn 1977) and in Paulchoffatiidae gen. et sp. indet. In all these cases I1 uniformly narrows towards the tip and there is no angulation or accessory cuspule. DORCM GS 10 described above differs in this respect also from paulchoffatiid I1. It may be I2 of a smaller species than the one to which I2 (DORCM GS 8, Pl. 4, fig. 1) described above belongs.

?Plagiaulacinae gen. et sp. indet., I3

Plate 1, figs 11, 14; Text-fig. 7

Material. DORCM GS 14 (sample 28) left I3 from the Cherty Freshwater Member of the Purbeck Limestone Formation, Sunnydown Farm Quarry near Langton Matravers.



TEXT-FIG. 7. ?Plagiaulacinae gen. et sp. indet.; DORCM GS 14, left I3; crown view; the buccal side is to the right. Scale = 1 mm.

Description. Left I3 DORCM GS 14, measured in anterior view is together with the root 2·7 mm long, the length of the root being 1·8 mm. The crown strongly overhangs the root. The tooth is three-cusped, compressed anteroposteriorly, 2·4 mm wide and 2·4 mm long in posterior view. The main cusp is steeply worn buccally and more horizontally worn lingually, producing a sharp triangular tip. A prominent anterior cusp is placed on the buccal side of the anterior wall of the crown, lower than the small cusp placed on the lingual side of the posterior slope. The latter is developed as a subhorizontal cingulum, the medial side of which extends upwards as a ridge towards the tip of the main cusp. In posterior aspect the crown is longer than anteriorly, producing a triangular tip upwards. The root is closed and bent posteriorly.

Comparisons. The three-cusped I3 characteristic of DORCM GS 14 occurs in both the Paulchoffatiidae (Hahn 1977) and Plagiaulacidae (Simpson 1928). DORCM GS 14 differs from I3 of all known paulchoffatiid taxa in having only one anterior cusp rather than two, the posterior cusp developed as a ridge, and in being compressed anteroposteriorly. It is more reminiscent of the I3 of *Henkelodon naias* and *Paulchoffatia* sp. (referred to by Hahn 1977, text-fig. 8 as *Kuehneodon* sp., but see Hahn 1978*b*, p. 183) than that of *Kuehneodon simpsoni*, although the posterior cusp, which is weak in our specimen, is hardly developed in *K. simpsoni*. DORCM GS 14 recalls I3 of *Bolodon crassidens* (Simpson 1928, text-fig. 11) in the arrangement of the cusps, but differs from it in being strongly compressed anteroposteriorly and roughly oval in cross section, rather than triangular, and in having less prominent additional cusps. It is also reminiscent of I3 of *Psalodon fortis* (Simpson 1929, p. 26, pl. 5, fig. 3), which although being two-cusped, is similar to DORCM GS 14 in being compressed anteroposteriorly. In this respect I3 of *P. fortis* differs from I2 which is laterally compressed. Our specimen differs from I3 of *P. fortis* (in addition to being smaller) in the presence of a prominent anterior cusp and a smaller posterior one. Because of this ambiguity we tentatively assign DORCM GS 14 to the Plagiaulacinae.

?Plagiaulacinae gen. et sp. indet., ?upper premolar or canine

Plate 5, figs 1–2

Material. DORCM GS 2 (sample 13) from Cherty Freshwater Member of the Purbeck Limestone Formation,

Sunnydown Farm Quarry near Langton Matravers, ?right anterior upper premolar ?P1, P2 or P3 or ?left canine.

Description. ?Upper premolar (DORCM GS 2) is 1·25 mm long and 1 mm wide in occlusal view. The roots are completely resorbed, but it cannot be excluded that the tooth was single-rooted. If so, it would be a canine rather than a premolar. There are three main cusps, two lingual and one buccal, and three smaller lingual cusps. One of them, the smallest, is placed at the corner of the anterior and lingual margins, the two remaining are on the posterior half of the lingual margin, the first of these being larger than the second. Along the anterior margin there are two minute cuspules, and the trace of a third one between them, while along the posterior margin there are two cuspules, the buccal one larger than the lingual. All the cusps are ornamented with radiating ridges. In grooves between the main cusps and between the two posterior lingual cusps there is an ornamentation of distinct pits.

Comparisons. The upper ?premolar (DORCM GS 2) is reminiscent of P1–P3 in the plagiaulacid genera *Bolodon* and *Ctenacodon* whose three main cusps are arranged similarly. We identify it tentatively as a right tooth, but it might be a left one. If so, the margin described here as anterior would be posterior and additional lingual cusps identified as posterior, would be placed anteriorly. We identify the side with additional cusps as lingual, by comparison with the position of main cusps in plagiaulacid upper premolars, in which two cusps are situated lingually and one buccally. This tooth differs from all the known plagiaulacid upper premolars in having additional cusps lingual to the three main cusps and anterior and posterior cuspules, and in having the pits in grooves between the cusps. Similar (but not certain if homologous) ornamentation (grooves and 'comma-shaped pits') occurs in molars of the Plagiaulacinae and Eobaatarinae but was not found previously in the anterior upper premolars. We assign DORCM GS 2 to the Plagiaulacinae, rather than to the Allodontidae or Paulchoffatiidae, because of this ornamentation. Another reason for this assignment is that the Allodontidae do not occur in the Purbeck of England, and the paulchoffatiids known from these beds do not fit the size of DORCM GS 2; they are too small. Additional cuspules on premolars occur rarely in the Paulchoffatiidae (e.g. in *Pseudobolodon* sp., Hahn 1977, text-fig. 3) and in the Plagiaulacidae (e.g. in *Bolodon elongatus*, Pl. 4, fig. 8). In both these taxa there are only two additional cuspules, but no lingual additional cusps as in DORCM GS 2 and the pits characteristic of our specimen are lacking. If DORCM GS 2 was single-rooted then it may be a canine rather than premolar, and the facet for contact with the adjacent tooth, which occurs on the side identified by us tentatively as the anterior one, would be for the contact with the first premolar, so indicating the posterior wall of the tooth. In such a case DORCM GS 2 would be a left rather than right tooth. However, uncontested canines have not been found so far in the Plagiaulacidae, although Hahn and Hahn (1983) tentatively suggested the presence of a canine in *Ctenacodon*. Canines occur in various paulchoffatiid genera, but we believe that the general structure of the described tooth has plagiaulacine rather than paulchoffatiid affinities.

Comparison of Plagiaulacinae species

Six plagiaulacine taxa have been described from the Purbeck Limestone Formation of England. These are: *Plagiaulax becklesii* Falconer, 1857; *Bolodon minor* (Falconer, 1857), assigned by Falconer (1857) to *Plagiaulax*; *Plioprion falconeri* (Owen, 1871), assigned by Owen (1871) to *Plagiaulax*, and referred to by us as '*Bolodon*' *falconeri*; *Bolodon crassidens* Owen, 1871; *Bolodon osborni* Simpson, 1928; and *Bolodon elongatus* Simpson, 1928.

B. osborni is known from both upper and lower jaws and dentition, and *Ctenacodon* cf. *minor* Simpson 1928 is regarded here as its junior subjective synonym. Three taxa, *Plagiaulax becklesii*, '*Bolodon*' *falconeri* and *Bolodon minor* are based on lower jaws, although upper premolars and molars are tentatively assigned to *B. minor* and described in this paper. Two taxa, *Bolodon crassidens* (Pl. 5, fig. 7; Text-fig. 5A) and *Bolodon elongatus* (Pl. 4, fig. 8), are based on maxillae with incomplete dentitions and the upper molars of both are not known. We agree with Hahn and Hahn (1983) that *Bolodon elongatus* possibly does not belong to the genus *Bolodon* and we therefore refer to it as '*Bolodon*' *elongatus*. Both *B. crassidens* and '*B*'. *elongatus* are relatively large and

correspond in size to the two large species based on the lower jaws. It is thus very probable that one of the large upper jaw taxa is conspecific with '*Bolodon*' *falconeri* and the other with *Plagiaulax becklesii*. If so, there would be four uncontested plagiaulacine taxa in the Purbeck of England (unless the ?upper premolar or canine, DORCM GS 2, described here as ?Plagiaulacinae gen. et sp. indet., belongs to a fifth plagiaulacine taxon).

If it were to be demonstrated in the future that *Bolodon crassidens* is conspecific with, e.g., *Plagiaulax becklesii*, then one should reconsider the generic assignment of *Bolodon osborni* and *Bolodon minor*, which would not be congeneric with *Bolodon crassidens*. As long as it cannot be demonstrated unequivocally which upper jaw matches the lower one, these taxonomic decisions cannot be made.

Bolodon minor is the smallest species of the genus. It differs from *B. osborni* in being smaller and in having ?four buccal cusps in p4 (one in *B. osborni*). The differences between p2 and p3 structure are hardly discernible (Text-fig. 3). Upper teeth of *B. minor* are poorly known, P5 DORCM GS 7 (Pl. 5, figs 8–9; Text-fig. 5C) and incomplete M1 DORCM GS 6 (Pl. 3, figs 1–2; Text-fig. 6B) described under cf. *B. minor*, differ from those in *B. osborni*: P5, in having two buccal cusps of equal size, while in *B. osborni* (Pl. 5, fig. 4; Text-fig. 5B) the posterior one is larger, and in having buccal cuspules less differentiated in size; M1, in having a nearly straight posterior margin, while it is convex posteriorly in *B. osborni* (Pl. 3, fig. 9; Text-fig. 6A) and possibly in having more and smaller buccal cusps. In spite of these differences *B. osborni* appears more closely related to *B. minor* than to *B. crassidens* (Pl. 5, fig. 7; Text-fig. 5A) and '*B*' *elongatus* (Pl. 4, fig. 8), from both of which it is also notably smaller. Both these latter species are known only from the anterior premolars. P1–P3 are similarly shaped in *B. crassidens* and in *B. osborni*, but P4 has two large buccal cusps in *B. crassidens* and a prominent cingulum buccal to them without cuspules, while there are three buccal cusps and a cingulum with cuspules in P4 of *B. osborni* (Text-fig. 5A-B). P4 in *B. crassidens* (Text-fig. 5A) more closely resembles P5 of *B. osborni* than P4 (Text-fig. 5B). P1–P3 in '*B*' *elongatus* (Pl. 4, fig. 8) differ notably from those in other *Bolodon* species in having a prominent posterior cingulum, P3 being smaller than P1 and P2, and elongated longitudinally. Lastly, both *B. minor* and *B. osborni* resemble '*Bolodon*' *falconeri* and differ from *Plagiaulax becklesii* in having four lower premolars rather than three.

DISCUSSION

English Purbeck Limestone Formation multituberculate mammals are known from four localities (Text-fig. 1): the previously known locality at Durlston Bay, Swanage, and three new localities (Ensom 1987, 1988): Sunnydown Farm and Lovell's Quarry, both near Langton Matravers, and Suttle's Quarry near Swanage. Multituberculates from the Durlston Bay locality are from the Marly Freshwater Member and those from the three new localities, the Cherty Freshwater Member, all within the Purbeck Limestone Formation. All the multituberculates described from Durlston Bay belong to the Plagiaulacinae (see 'Comparison of Plagiaulacinae species' above).

The new collection from Sunnydown Farm Quarry contains, in addition to some of the taxa previously known from Durlston Bay (*B. minor*, *B. osborni* and two large I2, possibly belonging to *Plagiaulax becklesii* or '*Bolodon*' *falconeri*), two new taxa: *Gerhardodon purbeckensis* gen. et sp. nov., and *Sunnyodon notleyi* gen. et sp. nov., both assigned to the Paulchoffatiidae. In addition we have described I3 assigned to the ?Plagiaulacinae, gen. et sp. indet., and an upper premolar or canine identified also as ?Plagiaulacinae, gen. et sp. indet. It appears from our study of the collection from Sunnydown Farm Quarry, that the English Late Jurassic multituberculate fauna was more diverse than previously thought. The new taxa differ from those previously known, by, among other features, notably smaller dimensions. This is, we believe, the result of a different sampling method. To find teeth less than 1 mm long (e.g. the holotype specimen of *Sunnyodon notleyi*) when searching for fossils in the outcrops would be difficult, but such small specimens are more readily collected using the washing and screening method adopted by us.

Evaluation of the fauna described in this paper in relation to the Middle to Late Jurassic and

Early Cretaceous multituberculates known from the world (see Kielan-Jaworowska 1974, and Clemens and Kielan-Jaworowska 1979, for earlier reviews) is of interest. The only Middle Jurassic multituberculate specimens so far known are an eroded ?I1 and an eroded ?molar, from Bathonian strata, the former from Oxfordshire (Freeman 1979) and the latter from Dorset (Freeman 1976), where in addition, a small undescribed fragment of what is possibly a multituberculate tooth (DORCM G 10827) was collected by one of us (P.C.E.). Due to the meticulous work of Hahn (1969, 1971, 1977, 1978*a*, 1978*b*, 1978*c*, 1988 and references therein; see also Hahn and Hahn 1983), the Late Jurassic (Kimmeridgian or Oxfordian, see Helmdach 1971 and Mohr 1989) multituberculate fauna of Portugal is well known, five genera being established, all assigned to the Paulchoffatiidae Hahn, 1969. Otherwise, Late Jurassic multituberculate faunas are known from the Purbeck of England (Simpson 1928 and references therein) and the correlative Morrison Formation of North America (Simpson 1929; Bakker and Carpenter, 1990; Engelmann *et al.* 1990). The Purbeck fauna is dominated by the Plagiaulacoidea which first appeared here. We have recognized two families within the Plagiaulacoidea: Plagiaulacidae with two subfamilies (Plagiaulacinae mostly for the European genera, but possibly occurring also in North America, and Eobaatarinae for Early Cretaceous European and Asian genera), and the family Allodontidae for the North American Late Jurassic genera. The genus *Bolodon* assigned by Hahn and Hahn (1983) to the Paulchoffatiidae, in our opinion, belongs to the Plagiaulacidae (Plagiaulacinae). As demonstrated in this study, rare and generally very small surviving members of the Paulchoffatiidae are also found in Purbeck strata.

From the Early Cretaceous (Barremian) (Mohr 1989) of Spain, isolated teeth are known (genus *Parendotherium* and *Plagiaulax*? sp.) assigned to the Paulchoffatiidae and Plagiaulacinae respectively (Crusafont Pairó and Adrover 1966; Crusafont and Gibert 1976; Hahn and Hahn 1983). The Early Cretaceous (Valanginian) English multituberculate *Loxaulax* (Simpson 1928; Clemens 1963; Clemens and Lees 1971) has been placed by Kielan-Jaworowska *et al.* (1987) in the Eobaataridae, regarded by us as a subfamily of the Plagiaulacidae.

Coeval with the Eobaatarinae there occurs in the Early Cretaceous of Asia a highly specialized family, the Arginbaataridae, assigned by us to a suborder *incertae sedis*. A single Early Cretaceous paulchoffatoid m1 assigned to a family of its own – the Hahnodontidae – has been recently found in North Africa (Sigogneau-Russell 1991). A large collection of isolated multituberculate teeth was obtained many years ago from the Albian of Texas (Patterson 1956; Slaughter 1965) and is currently being described by Krause and others (see Abstract by Krause *et al.* 1990). Early Cretaceous multituberculates have also recently been recovered from Cloverly Formation localities in Montana by D. W. Krause and R. Cifelli (personal communication from D. W. Krause to Z.K.-J.).

It follows from the foregoing review that Middle to Late Jurassic and Early Cretaceous multituberculates are scarce and poorly known. The relationships between the suborders Paulchoffatoidea and Plagiaulacoidea and between them and members of the two later multituberculate suborders Taeniolabidoidea and Ptilodontoidea are still poorly understood. We believe that continuing study by one of us (P.C.E.) of samples from the Purbeck Limestone Formation and the resultant study of the morphology and enamel microstructure of the teeth may contribute to a better understanding of multituberculate phylogeny and interrelationships among the multituberculate suborders.

Acknowledgements. Mr W. T. Haysom drew the attention of one of us (P.C.E.) to the quarries at Sunnydown Farm. The excavation of this site was carried out with permission from the owners Mr and Mrs R. F. Notley and was funded by the Dorset Natural History and Archaeological Society who have given permission for the authors to study the material collected. Access to other quarries was granted by Messrs P. Lovell and C. Suttle. The Area Museum Council for the South West gave grant-aid for the sieving machine that was built and installed at the Dorset County Museum by Mr S. M. Etches. The latter, along with S. Baker, A. and P. Blackler, A. Brokenshire, Mrs M. Ensom, S. Riley, R. Road, S. Roles, J. Seabrook, P. Stevens, Mrs J. Thomas and W. Wilblood helped P.C.E. with the excavations. Mrs H. Machen and Mrs C. Cook gave great assistance with the sieving, and G. Bate with the picking of residues.

During the course of this study we compared casts of Late Jurassic multituberculates from England, housed in the BMNH collection, and from North America housed at the YPM collection, sent to Z. K.-J. in 1986 by Dr J. J. Hooker and Professor J. Ostrom respectively. Z. K.-J. was able to study a large collection of casts of various multituberculates housed at the Department of Anatomical Sciences of the State University of New York at Stony Brook, in charge of Professor D. W. Krause. Professors J. A. Hopson (Chicago), G. Hahn (Marburg) and D. W. Krause (Stony Brook) read the manuscript of this paper and provided most useful comments. The SEM micrographs were taken by Z. K.-J. and Ms T. Rolfsen (Institute of Biology, University of Oslo), and the drawings prepared by Mr B. Bocianowski after Z. K.-J. pencil sketches. Research of Z. K.-J. was supported by funds from Norges Allmennvitenskapelige Forskningsråd (grant ABC/LR 441. 90/002). To all these persons and institutions we express our sincere thanks and gratitude. This paper is Contribution No. 363 from the Paleontological Museum, University of Oslo.

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Typescript received 12 September 1990
Revised typescript received 27 February 1991